SEASONAL MOVEMENTS AND HABITAT USE OF RAINBOW TROUT IN THE SUSITNA RIVER BASIN, SOUTHCENTRAL ALASKA

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Abstract

Potamodromous Rainbow Trout are an important ecological and recreational resource in freshwater systems of Alaska, and increased human development, hydroelectric projects, declining Pacific salmon stocks, and climate change may threaten their populations. We used aerial and on-the-ground telemetry tracking, field-measured and remotely-sensed aquatic habitat characteristics, snorkel surveys, and resource selection and occupancy models to characterize seasonal movements and habitat use of adult Rainbow Trout (>400 mm FL) at multiple spatial and temporal scales across the large (31,221 km^2) and complex Susitna River basin of southcentral Alaska during 2003-2004 and 2013-2014. We found that trout overwintered in mainstem habitats near tributary mouths from November to April. After ice-out in May, trout ascended tributaries up to 51 km to spawn, and afterward moved downstream to lower tributary reaches to intercept egg and flesh subsidies provided by spawning salmon in July and August. Trout transitioned back to mainstem overwintering habitats at the onset of autumn when salmon spawning activity waned. Fidelity to tributary of capture varied across seasons, but was high in three out of four drainages. Different habitat characteristics influenced Rainbow Trout habitat use during each season, including stream gradient and sinuosity in the winter, substrate suitability and sinuosity during spawning, mean annual flow during the pre-salmon feeding season, and Chinook salmon spawning potential after the arrival of adult salmon in freshwater. We found that during the ice-free feeding season trout responded to fine-scale (channel unit) characteristics rather than more coarse-scale (stream reach) variables. Weekly movements were significantly longer when spawning salmon were present compared to pre-arrival. We found no difference in movements and habitat use for a subset of fish for which sex was identified using genetic analysis. However, the observed sex ratio was heavily female-biased, which contrasts with what has been observed in other non-anadromous salmonid populations. As most trout undertake extensive movements within and among tributaries and make use of a variety of seasonal habitats to complete their life histories, it will be critical to take a broad and multi-scale approach to their management in light of anticipated future land use and climate change.

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Introduction

Seasonal movements and habitat use

Many animals utilize a variety of habitats during different stages of their life histories, and undertake movements (travel between different habitat types) or migrations (predictable round-trip movements undertaken by the majority of a population) on a periodic or seasonal basis (Alerstam et al. 2003; Dingle and Drake 2007). Typically, animals remain in areas that maximize growth, survival, and reproductive success. For example, juveniles may spend time in rearing areas with adequate food and protection from predators and harsh environmental conditions (Beck et al. 2001). Adult life stages may move among habitats that maximize energy intake (feeding zones), areas that are suitable for successful reproduction (reproductive or spawning zones), and habitats that minimize exposure to predators or harsh environmental conditions (refugia or overwintering zones; Northcote 1978; Schlosser and Angermeier 1995; Lucas et al. 2001). Complex life histories and use of multiple habitat types are characteristic of salmonid fishes (e.g., salmon and trout), and in adults seasonal movements among spawning (once a year or once every few years), feeding, and overwintering (refugia) habitats following an annual or biennial cycle are common, although the distance traveled among these habitats may vary by species and life stage. Examples include long-distance (10^1-10^3 km) migrations between salt- and freshwater habitats (diadromy), and more localized movements among habitats in freshwater (potamodromy; Northcote 1997). Potamodromy has been observed in whitefishes (*Coregoninae*), grayling (*Thymallinae*), and many species of the subfamily *Salmoninae* including Rainbow Trout (*Oncorhynchus mykiss*). Evaluating habitat use and movements analysis across multiple spatial and temporal scales is critical to identify patterns that may be overlooked at a single scale (Frissell et al. 1986; Fausch et al. 2002). Although some previous research examined habitat use and movements of potamodromous Rainbow Trout (Meka et al. 2003; Schwanke and Hubert 2003), specific seasonal habitat types used, relative to what is available, and relationships with spawning salmon have yet to be quantified.

Sex bias

Habitat use and movements within a species or population of animals may differ between sexes (Pusey 1987; Perrin and Mazalov 2000). In fishes, females generally have higher energetic demands relative to males owing to the cost of producing eggs. By comparison, sperm

production in males requires relatively little energy (Hutchings and Gerber 2002). Additionally, female fish typically experience less intrasexual competition for mating opportunities (Cano et al. 2008) As a result, females may spend more time in feeding habitats and exhibit risky behaviors to maximize energy input, make shorter spawning movements and have smaller home ranges to minimize energy expenditure, or display infrequent reproductive events because of high caloric thresholds. Conversely, males may spend less time feeding, have larger home ranges, undertake longer exploratory movements and reproductive migrations, or have more frequent reproductive efforts. In non-anadromous salmonids, a male-biased strategy is typically seen where males are opportunistic and may range far and wide in search of food or mates (Hutchings and Gerber 2002; Olsen et al. 2006), although there are exceptions to this pattern (Koizumi et al. 2006). It is likely that potamodromous Rainbow Trout also exhibit a male-biased movement strategy because reproductive success of males may be limited by the number of available mates, thus individuals may travel long distances between spawning groups to fertilize the eggs of multiple females. In contrast, female trout are required to invest more energy into production of gametes, and may not be limited by the amount of food or number of mates available (thus having little incentive for movements to other areas and showing higher spawning stream fidelity).

Research objectives and implications

Chapter one investigates annual seasonal movements and habitat utilization across four Alaska subpopulations of native potamodromous Rainbow Trout, with comparisons among sexes and tributaries. Analyses were based on monthly trout location and movement data collected through aerial radio telemetry, characterization of broad-scale physical and biological characteristics of seasonal habitats calculated from a digital landscape model, and genetic sex identification for a subset of tagged fish. We hypothesized that trout movement among tributaries would occur at low prevalence, some individuals would undertake long-range movements, and males would undertake longer movements than females during feeding and spawning seasons in order to take advantage of additional opportunities. Finally, we predicted trout would use multiple habitat types (e.g., mainstem, tributaries, headwaters; Bartlett and Hansen 2000) seasonally according to their availability, and males and females would select different habitats given differential energetic demands among seasons and between sexes similar to findings of Hutchings and Gerber (2002).

The goal of chapter two was to gain a better understanding of how fine-scale habitat utilization and movements of an Alaska subpopulation of indigenous potamodromous Rainbow Trout during the open-water feeding season (June to September) relate to the presence of spawning salmon. Our analyses were based on locations, occupancy, and movement data collected through weekly radio telemetry and snorkel surveys, characterization of multi-scale physical and biological characteristics of seasonal habitats surveyed in the field and calculated from a digital landscape model, and genetic sex identification of tagged fish. We hypothesized that trout movements would decrease after the arrival of spawning salmon because of the spatially concentrated nature of salmon-derived subsidies (e.g., eggs and sloughed flesh; Scheuerell et al. 2007), and that males would undertake longer movements than females in search of feeding habitats. Finally, we predicted trout would select habitats at all spatial scales with high complexity for cover (large woody debris, sinuosity) and with spawning salmon present in order to capitalize on food subsidies.

Identification of the context within which critical habitats are defined, across broad landscapes, is an important tool to better monitor, manage, and conserve stream fish populations (Schlosser and Angermeier 1995; Wiens 2002; Naiman and Latterell 2005). Analysis of habitats and movements at multiple spatial and temporal scales is essential because many species (e.g., potamodromous Rainbow Trout) carry out their life histories across scales, and important habitat parameters may be excluded when focusing on only one level (Frissell et al. 1986; Schlosser 1991; Fausch et al. 2002). Combining continuous field measurements of local habitats with reach and watershed-scale metrics to predict the location of a target species is an effective way to quantify how available habitats are used (Walter 2012; Cram et al. 2013). The resulting fish-habitat relationships can be applied to other watersheds via resource selection modeling (Manly et al. 2002) to predict where important habitat occurs.

Recent and impending human development in Alaska will likely have an effect on fish populations, including Rainbow Trout. Proposed hydroelectric projects may have long-reaching effects on aquatic ecosystems, including Rainbow Trout and salmon (AEA 2013). Future anthropogenic land development (expected to double within the next 50 years in some regions) may cause greater sedimentation, thinning of important riparian zones and increased sportfishing pressure (Schick 2006; MSBSHP 2013). Climate change may affect seasonal timing, water

temperatures, and allow for invasion of non-native species (Prowse et al. 2006). In light of these threats, it is necessary to gain an understanding of the movements and habitat utilization of potamodromous Rainbow Trout in Alaska to identify potential issues that may affect this economically and ecologically important species. Results of this work could be applied to similar drainages in Alaska to identify critical trout habitats and may be useful for resource managers as baseline knowledge and for prioritizing habitat protection efforts in light of anticipated future land use and climate change.

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Chapter 1: Seasonal movements and habitat use of potamodromous Rainbow Trout in the Susitna River basin, southcentral Alaska[1]

Abstract

Potamodromous Rainbow Trout are an important ecological and recreational resource in freshwater systems of Alaska, and increased human development, hydroelectric projects, declining Pacific salmon stocks, and climate change threaten their populations. We used aerial and on-the-ground telemetry tracking and resource selection models to characterize seasonal movements and habitat use of adult Rainbow Trout (>400 mm FL) across the complex, large (31,221 km^2) Susitna River basin of southcentral Alaska during 2003-2004 (N = 148) and 2013-2014 (N = 84). We found that trout overwintered in mainstem habitats near tributary mouths from November to April. After ice-out in May, trout ascended tributaries up to 51 km to spawn, and afterward moved downstream to lower tributary reaches to intercept egg and flesh subsidies provided by spawning salmon in July and August. Trout transitioned back to mainstem overwintering habitats at the onset of autumn when salmon spawning waned. Among tributaries where trout were initially tagged, fidelity varied across seasons, but was high in three out of four drainages. Different habitat characteristics influenced Rainbow Trout habitat use during each season, including most notably stream gradient and sinuosity in the winter, substrate suitability and sinuosity during spawning, mean annual flow during the pre-salmon feeding season, and Chinook salmon spawning habitat intrinsic potential after the arrival of adult salmon in freshwater. We found little difference in overall movements and habitat use for a subset of fish for which sex was identified using genetic analysis. However, the observed sex ratio was heavily female-biased, which contrasts with what has been observed in other salmonid populations. As most trout undertake extensive movements within and among tributaries and make use of a variety of seasonal habitats to complete their life histories, it will be critical to take a broad-scale approach to their management in light of anticipated future land use and climate change.

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INTRODUCTION

Most fishes utilize a variety of habitats to complete their life histories, and undertake movements (travel among different habitat types) or migrations (predictable round-trip movements undertaken by a majority of a population) of variable lengths on a periodic or seasonal basis (Alerstam et al. 2003; Dingle and Drake 2007). For example, juveniles often rear in areas with adequate food and protection from predators and harsh environmental conditions (Beck et al. 2001). Adult life stages may move seasonally among habitats that maximize energy intake (feeding zones), areas that are suitable for successful reproduction (reproductive or spawning zones), and habitats that minimize exposure to predators or harsh environmental conditions (refugia or overwintering zones; Northcote 1978; Schlosser and Angermeier 1995; Lucas et al. 2001). Complex life histories and use of multiple habitat types through ontogeny are characteristic of salmonid fishes (e.g., salmon and trout), and in adults, seasonal movements among habitats following an annual or biennial cycle are common (Northcote 1997). Quantifying the locations of these seasonal habitats, and the connections among them, is critical for species management, particularly when habitats extend across multiple jurisdictions or management entities (Temby et al. 2015).

Fish movement patterns vary from uniform short-distance dispersal to directional long-range travel, even within populations (Gowan et al. 1994; Rodriguez 2010). Examples include long-distance (10^1-10^3 km) migrations between salt- and freshwater habitats (diadromy), and more localized movements (10^0-10^1 km) among habitats and multiple tributaries in freshwater (potamodromy; Northcote 1997). Potamodromy has been observed in many species of the subfamily *Salmoninae* including Rainbow Trout (*Oncorhynchus mykiss*; Meka et al. 2003; Schwanke and Hubert 2003). In salmonids, movement patterns vary between populations, life stages, and seasonally, with movements often triggered by environmental cues such as changes in photoperiod, flow, turbidity, or temperature (Hilderbrand and Kershner 2000; Mellina et al. 2005). In stream fishes it is common to observe a leptokurtic pattern where the majority of a population make short movements away from core habitat areas with a smaller proportion of individuals moving long distances (Gowan et al. 1994; Skalski and Gilliam 2000; Radinger and Wolter 2014). To date, study of movement patterns in stream fishes has been limited to specific life stages, yet remains to be quantified across seasons for individuals where the impetus for movement (e.g., spawn, rear, or take refuge) may vary considerably.

Habitat use and movement patterns within a species or population of fish may differ between sexes (Pusey 1987; Perrin and Mazalov 2000). In freshwater non-anadromous salmonids, females generally have higher energetic demands relative to males owing to the cost of egg production (Koizumi et al. 2006). By comparison, sperm production in males requires relatively little energy (Hutchings and Gerber 2002). Additionally, female fish experience less intrasexual competition for mating opportunities (Cano et al. 2008). As a result, females may spend more time in feeding habitats where they exhibit risky behaviors to maximize energy input, make shorter spawning movements to minimize energy expenditure resulting in smaller home ranges, or display infrequent reproductive events (e.g., skipped spawning) owing to high caloric thresholds (Hutchings and Gerber 2002). Conversely, males may spend less time feeding, have larger home ranges, undertake longer exploratory movements and reproductive migrations, or have more frequent reproductive efforts. In non-anadromous salmonids, a male-biased strategy is often observed where opportunistic males may range far and wide in search of food or mates (Hutchings and Gerber 2002; Olsen et al. 2006), although there are exceptions to this pattern (Koizumi et al. 2006). Consequently, non-anadromous salmonid movements and habitat use may vary by sex, although there is a paucity of studies on this topic in the literature (Hutchings and Gerber 2002; Koizumi et al. 2006).

Even in Alaska, typically considered to contain relatively pristine ecosystems, management of highly mobile stream fish populations such as potamodromous Rainbow Trout is complicated owing to the uncertainty resulting from potential anthropogenic impacts and climate change (Prowse et al. 2006). Additionally, Rainbow Trout are highly sought-after as sport fish throughout their native range in western North America, where fishing pressure can be heavy in drainages that are easily accessible by road (Bartlett and Hansen 2000; Jennings et al. 2011). Moreover, in basins where Rainbow Trout and Pacific salmon (*Oncorhynchus* spp.) co-occur, trout populations may be highly dependent on spawning salmon-derived food sources (e.g., eggs and decomposing flesh) to meet energetic demands through periods of low food availability (winter months; Scheuerell et al. 2007). Because Pacific salmon runs are generally declining along the western coast of North America (Hilborn 2013), trout populations that depend on these subsidies may be negatively impacted. In addition, land development (increasing in Alaska) may put pressure on populations owing to increased sedimentation, thinning of riparian zones,

increased sportfishing pressure, and altered flow and temperature regimes and loss of habitat connectivity from installation of culverts and hydropower dams (AEA 2013; MSBSHP 2013). As a result, a better understanding of seasonal habitat use and movements of potamodromous Rainbow Trout is warranted.

In light of these threats, our overall goal was to gain a better understanding of the movements and habitat utilization of an Alaska population of native potamodromous Rainbow Trout to provide information to better protect these economically and ecologically important fish. Our analyses were based on trout location and movement data collected through radio telemetry, characterization of broad-scale physical and biological characteristics of seasonal habitats calculated from a digital landscape model, and genetic sex identification for a subset of tagged fish. Our specific objectives were to 1) characterize movement patterns by trout within and among mainstem and tributary streams; 2) quantify how these movements varied seasonally, annually, and between sexes; and 3) identify important seasonal habitats across a complex Alaskan riverscape. We hypothesized that trout movement among tributaries would occur at low prevalence, some individuals would undertake long-range movements, and males would undertake longer movements than females during feeding and spawning seasons in order to take advantage of additional opportunities. Finally, we predicted trout would use multiple habitat types (e.g., mainstem, tributaries, headwaters) seasonally according to their availability, and males and females would select different habitats given differential energetic demands among seasons and between sexes.

METHODS

Study area.—The Susitna River basin (31,221 km^2) consists of a large network of glacial and clearwater streams in southcentral Alaska that originate in the Alaska Range and Talkeetna Mountains and ultimately form the 482 km Susitna River (Figure 1.1; Barrick et al. 1983), which drains into the Upper Cook Inlet of the Gulf of Alaska. The Susitna River is the 15th largest river in the United States in terms of discharge (Kammerer 1990). The basin is home to large, economically and ecologically important indigenous populations of potamodromous Rainbow Trout. Future anthropogenic land development (expected to double within the next 50 years; Schick 2006) in the Matanuska-Susitna region as well as the proposed Susitna-Watana Hydropower Project (AEA 2013) may affect trout, Arctic Grayling (*Thymallus arcticus*), and Pacific salmon in the Susitna basin (MSBSHP 2013). For this study, trout were tagged in the

drainages of four westward flowing tributaries of the Lower Susitna River basin originating in the Talkeetna Mountains (Figure 1.1); one with glacial influence, the Kashwitna River (61°59'7"N, 149°50'57"W), and three runoff-fed streams: Willow Creek (61°46'44"N, 150°9'5"W), Montana Creek (62°6'18"N, 150°3'48"W), and Chunilna (Clear) Creek (62°22'15"N, 150°0'59"W). Kashwitna River trout were predominantly tagged in the clear-water North Fork, but the remainder of the Kashwitna drainage is heavily influenced by glacial melt. Discharge and turbidity in the Susitna River are highest in June and July at the peak of glacial melt, and lowest when flow contribution from glacial melt recedes during fall and early winter (Figure 1.2). Discharge patterns differ among tributaries, with peaks occurring during snowmelt runoff in May and June and following frequent precipitation events in August and September (Figure 1.2). Lotic habitats in the Susitna River basin are typically ice-covered from October to April, although open-water leads may occur in areas with swift current or groundwater upwelling. The Susitna River and its tributaries have similar thermal regimes, with lowest temperatures in winter and a peak in midsummer (Figure 1.2).

The Susitna River basin contains substantial spawning populations of Chinook Salmon (*O. tshawytscha;* the fourth largest run in the state of Alaska; Hasbrouck and Edmundson 2007), Pink Salmon (*O. gorbuscha*), Chum Salmon (*O.keta*), Sockeye Salmon (*O. nerka*), and Coho Salmon (*O. kisutch*). Salmon and Rainbow Trout populations are the targets of a popular sportfishery (Yanusz 2009). Angling for Rainbow Trout in the Susitna River basin is mostly catch-and-release, and trout may be subjected to heavy pressure from fly fishermen during summer months (June to September). For example, in 2010 the estimated total catch of Rainbow Trout by recreational anglers in the lower basin was 60,770 fish, with 2,260 trout harvested across 122,235 angler-days (Jennings et al. 2011).

Fish capture and tagging.—Adult Rainbow Trout (>400 mm FL) were captured in 2003 in the four tributaries and in Willow Creek alone in 2013 and 2014 via fly-rod-and-reel angling methods. Capture efforts occurred in the late summer-early fall in lower tributary reaches. Fish eligible for surgery were landed quickly with a net and immersed in an anesthetic bath until stage 3-4 anesthesia was attained (Summerfelt and Smith 1990). In 2003 spearmint oil was used as an anesthetic (Yanusz 2009), in 2013 clove oil was used, and in 2014 AQUI-S^{TM} 20E (AQUI-S New Zealand Ltd, Wellington, New Zealand) was employed per permit stipulations. Trout with visible injuries or those showing signs of lethargy and exhaustion were rejected as surgical

candidates and immediately released. Anesthetized fish were placed ventral-side up in a moist neoprene-lined cradle for surgery. A crew member continuously delivered anesthetic and oxygenated water to the fish's gills with a turkey baster and monitored rapidity of gill movements and movement of the fish for the duration of the surgery. A separate crew member conducted the surgery, first making a small 2-cm incision 1-2 cm off the mid-ventral line about 3-4 cm anterior of the pelvic girdle with a scalpel sterilized in Betadyne solution. A grooved rod was then inserted into the incision and towards the posterior of the fish. Next, a hollow 16-gauge needle was inserted into the fish just behind the pelvic girdle, and directed along the grooved rod until the tip reached the incision (Ross and Kleiner 1982). The antenna wire of a radio transmitter (F1835C in 2013 and 2014, 17x44 mm, 14 grams, battery life capacity 483 days; FI830 in 2003, 12x53 mm, 11 grams, battery life capacity 340 days; Advanced Telemetry Systems, Isanti, MN) was then threaded through the fish via the hollow needle, and a radio tag was inserted, bottom first, into the incision site while using the transmitter wire to help position the tag in the fish. After the tag was inserted into the body cavity of the trout, the incision was closed with three to four 3-0 PDS™ monofilament absorbable sutures about 3.2 mm apart. After suturing, the wound was dried with sterile gauze and a few drops of Vetbond™ surgical glue were applied. Vetbond™ takes about 10 seconds to dry, at which time mucous from an adjacent area of the fish was smeared onto the wound to facilitate healing. After each trout recovered from surgery in an aerated basin of fresh river water, a right pelvic fin clip was taken for genetic sex identification, and a numbered Floy™ FD-94 T-bar anchor tag was implanted at the base of the dorsal fin as an external identifier. Individuals were visually examined and the presence of any physical deformities likely caused by angling (e.g., hooking scars including lacerations, jaw deformities, damaged mandibles, and dysfunctional eyes) was noted. Fully-recovered fish were released into a pool or other low-velocity habitat near the site of capture. Surgical tools were sterilized in an iodine-povidine solution and rinsed with a saline solution between each surgery.

Fish tracking.—Monthly fixed-wing aerial surveys were conducted from October 2003 to October 2004 and January to December 2014 during which locations of radio-tagged Rainbow Trout were identified using an Advanced Telemetry Systems (ATS) model R4500C telemetry receiver. Flights were exhaustive and covered the majority of the Lower Susitna River basin mainstem and tributaries from upper Chunilna Creek in the north to Cook Inlet in the south (Figure 1.1). Weekly ground tracking of fish along Willow and Deception Creeks substituted for

aerial tracking during July and August 2014 when no flight surveys were flown. Ground tracking was undertaken via raft and on-foot, and an ATS model R4500C telemetry receiver attached to a Yagi antenna was used to pinpoint and record fish locations (K. M. Fraley, unpublished data). Transmitter identification number, latitude, longitude, signal strength, and presence/absence of a mortality code were recorded for all surveys. Exact trout locations for each survey were determined based on the highest signal strength reported by the telemetry receiver. Fish mortality was classified by either a mortality signal given off by an inactive radio transmitter (internal tag motion-sensor, triggered by 24 hours or more of inaction), or by failure to locate the fish after two or more surveys of the study area. Post-tagging (e.g., initial) mortality was assumed when a fish gave repeated mortality signals or permanently disappeared from the study area during the first two telemetry surveys after tagging (Appendix 1.A).

Genetic sex identification.—Pelvic fin clips were taken from each radio-tagged trout captured in Willow Creek in 2013-2014 and stored in 95% ethanol. DNA was isolated in the laboratory using a DNeasy Blood & Tissue Kit (Qiagen, Inc., Hilden, Germany) and electrophoresed to verify success of extraction. Genomic DNA was used as a template in PCR reactions using primers OmyY1 F (5'-GTTCATATGCCAGGCTCAAC-3') and OmyY1 R (5'-CGATTAGAAAGGCCTGCTTG-3') following methods of Brunelli et al. (2008). Primers targeting salmonid mitochondrial genome fragments were used as a DNA quality control. All PCR products were dyed and examined using agarose gel electrophoresis. The resulting bands (viewed under UV light) were examined to determine the sex of each fish (See Figure 1.3 for an example of sex identification final electrophoresis gel). Samples exhibiting horizontal bands at 792 base pair length were designated as a male and those without bands at this location as female. Fin clips were also taken from three known female Rainbow Trout from the Alaska Department of Fish and Game's Ruth Burnett Sport Fish Hatchery in Fairbanks, Alaska and three male Rainbow Trout from the Montana Fish, Wildlife, and Parks' Murray Springs Trout Hatchery near Eureka, Montana to serve as controls and verify the accuracy of the sex identification analysis. Each sample was processed 2-3 times to ensure precision of the analysis. A simple binomial test was employed to determine if the sex ratio departed from 1:1.

Fish locations, movement, and tributary fidelity.—Rainbow Trout locations were imported into a geographic information system (GIS) using ArcMap (ver. 10.1; Environmental Systems Research Institute, Redmond, California) and snapped to the nearest stream polyline in a digital

landscape model (NetMap; Benda et al. 2007) parameterized for the Matanuska-Susitna river basin. The NetMap model generates an analytic digital stream network layer based on a remotely-sensed digital elevation model (DEM) comprised of 50-200 m stream reaches which are linked to the surrounding landscape and attributed with geomorphic characteristics (e.g., gradient, stream width, drainage area, etc.; Clarke et al. 2008; Bidlack et al. 2014). The Matanuska-Susitna River basin DEM was based on synthetic aperture radar (SAR; 5-m res) and light detection and ranging (LIDAR; <1-m res) imagery. We used NetMap instead of the National Hydrography Dataset (NHD; USGS 2013) for the state of Alaska because the current Alaska NHD is low quality relative to data available for the contiguous U.S. (e.g., coarser scale, misrepresented flow lines, disconnected and omitted streams). Based on 2004 and 2014 data, individual fish locations assessed via aerial telemetry were determined to be accurate within 0.5 km based on a comparison of GPS locations from aerial tracking with known on-the-ground points from stationary telemetry tags (R. Yanusz and K. M. Fraley, unpublished data). As a result, we aggregated the 50-200 m NetMap digital stream reaches to 0.5 km reaches to which we assigned fish locations.

Fidelity to tributary of capture was assessed by counting the number of fish that remained in, or returned to, the tributary of capture relative to those that spawned or fed in other locations (Northcote 1997). The overwintering season was not included because the majority of fish occupied the mainstem Susitna or Talkeetna Rivers during this time, and thus were not associated with any particular tributary (see Results). We classified overwintering, spawning, and feeding seasons based on general life history information for Rainbow Trout in Alaska (Bartlett and Hansen 2000; Yanusz 2009) as follows: the overwintering season was October through early May when Susitna River basin streams are ice-covered, the spawning season was immediately following ice-out in mid-May to the cessation of spawning activities in early June, and the feeding season was the open-water season from June to September. We split the feeding season into two seasons (early and late feeding) to investigate the potential difference in trout movement and habitat use before and after the arrival of spawning salmon (Hasbrouck and Edmundson 2007). The proportion of complex movements, defined as movements by a fish between multiple tributaries or movement away from the home tributary over multiple seasons, was also calculated for each tributary and year. An example of a complex movement would be a

trout tagged in Tributary A moving to Tributary B during the spawning season, then moving to Tributary C for the early feeding season, and returning to Tributary A during late feeding season.

Inter-seasonal movement distances (ISM; km) for individual fish were measured in ArcMap for each tributary, season, and year (Meka et al. 2003). Total annual movements (TAM; km) were calculated by summing the ISM distances for individual fish that were determined to be alive from the overwintering season through late feeding season for each tributary and year (Schwanke and Thalhauser 2011). Distance from confluence of the tributary of capture (DFC; km) was calculated for all individual fish locations by season, year, and tributary (Meka et al. 2003).

Data analysis.—We compared Rainbow Trout TAM, ISM, and DFC among the four tributaries, two years (2004 and 2014), four seasons (overwintering, spawning, early and late feeding), and by sex using two-factor analysis of variance (ANOVA). If significant differences were detected by the ANOVA, we used Tukey's HSD post-hoc test for multiple comparisons. To address the potential for bias induced by non-normality of data we compared results of the ANOVA with those of a randomized permutation test (Manly 2006) based on the same main effects. Results of the permutation test were identical to the two-factor ANOVA. Based on those results, we felt justified that proceeding with the ANOVA analysis would not substantially influence the interpretation of our results.

We used resource selection functions (RSF; Manly et al. 2002; Johnson et al. 2006; Lele 2009) to quantify Susitna River basin Rainbow Trout habitat selection during the overwintering, spawning, early feeding, and late feeding seasons. The RSF approach determines resource selection by comparing characteristics of used locations (i.e., seasonal habitats) to available ones based on weighted distribution theory (Johnson et al. 2006) and an exponential resource selection function (Manly et al. 2002). We limited the study extent (i.e., set of "available" stream reaches) to reaches with upstream drainage area >12.5 km^2 as no trout were ever observed in smaller streams.

Covariates used in the RSF analysis were riverscape-scale habitat attributes calculated continuously across the study extent in the Matanuska-Susitna river basin using NetMap. Attribute values from 50-200 m NetMap reaches were aggregated (i.e., averaged across) to the 0.5 km scale (see above) to better match telemetry location accuracy. Animal location accuracy is vital for producing and evaluating RSF models (Morehouse and Boyce 2013). We chose five

attributes to represent physical and biological habitat factors potentially important to Rainbow Trout within and among seasons. The first attribute, channel gradient (GRAD; %) was generated by NetMap based on the underlying DEM (Clarke et al. 2008). Stream gradient can serve as a barrier to upstream movements and influences streamflow velocity and hydraulic characteristics such as upwelling and downwelling, and has implications for fish energy expenditure (i.e., swimming speed), delivery of dissolved oxygen to all life stages, and food resources to juveniles and adults. We predicted that gradient would be important over all seasons owing to the propensity for fish to seek areas of optimal flow, food, and dissolved oxygen availability for refugia, spawning, and rearing (Walter 2012; Cram et al. 2013).

The second attribute, sinuosity (SINU; unitless), is a ratio of the magnitude of meandering of a stream across its floodplain. Sinuosity is calculated by dividing the stream channel path length between two points along the stream (i.e., in-stream distance) by the shortest path length between those points (i.e., Euclidean distance). The metric ranges from 1 (least sinuous) to infinity (most sinuous; Friend and Sinha 1993). Sinuosity was calculated in NetMap with a channel path length equal to 40 times the channel width (Rosgen 1994). Similar to gradient, sinuosity affects stream flow as well as substrate size and bed load movement and spawning salmon potential (Wirth et al. 2012). In addition, increased sinuosity typically results in higher aquatic habitat complexity and is indicative of a stream channel unaltered by human development (Fausch and Northcote 1992). Thus, sinuosity is likely important for Rainbow Trout habitat selection over all seasons, particularly during late feeding season when trout are likely seeking salmon spawning areas to take advantage of food subsidies.

We also chose mean annual flow (MAF; 1000 m^3/s) as a relative measure of stream size (Clarke et al. 2008). This metric was calculated using NetMap based on an equation for southcentral Alaska (Brabets 1996) where:

$$MAF = (1.025 * A^{0.024} * P^{1.186}) / 1000,$$

Where P is mean annual precipitation (mm) and A is upstream drainage area (km^2). MAF was converted to units of 1000 m^3/s to force model-averaged parameters to be informative. Flow is likely important to Rainbow Trout across seasons as they seek out areas with velocity that minimizes energy expenditure but adequately delivers drifting food items to juveniles and adults and dissolved oxygen to eggs (Bisson et al. 1988). Stream size is likely also important because

salmonids are known to occupy larger stream reaches (except during spawning), and avoid high-gradient smaller reaches to take advantage of additional cover protecting from terrestrial and aerial predators (Walter 2012).

We included a binary variable for predicted median substrate size (D50; mm) as a habitat variable for Rainbow Trout spawning season. This metric was calculated by NetMap based on bed shear stress: the depth-slope product using channel gradient, bankfull flow depth, and water density. The relationship between bed shear stress and D50 was taken from a regional model for the Pacific Northwest (Buffington et al. 2004). We developed a binary predictor to represent reaches suitable (1; D50 = 15-25 mm; Kondolf and Wolman 1993), and unsuitable (0; all other values of D50). Substrate size is known to be important for spawning salmonids because substrate that is too fine is less likely to allow dissolved oxygen and wastes to be delivered or removed from interstitial spaces where eggs are deposited. However, substrate that is too large may crush eggs or allow them to be dislodged, and may give predators easier access (Kondolf and Wolman 1993).

Finally, we included a measure of Chinook salmon spawning habitat potential as a candidate predictor of trout use during the late feeding season (CHINIP). This metric was based on a habitat intrinsic potential model (IP) methodology developed by Burnett et al. (2007), and parametrized for spawning Chinook salmon in the Columbia River basin (Busch et al. 2011). An IP model for Chinook spawning habitat potential has yet to be developed for the Susitna River basin. The IP is a unitless metric that ranges from 0 to 1 and represents the potential of a given reach to provide habitat for spawning Chinook salmon. The metric is based on three geomorphic variables that influence the physical processes that shape channel form: channel confinement (unitless ratio of floodplain width to bankfull channel width), channel width (m), and channel gradient (%). These variables were calculated using NetMap. The IP covariate was then calculated in NetMap for each reach based on preference curves from Busch et al. (2011). Reaches with high Chinook spawning IP are likely selected for by Rainbow Trout during the late feeding season because trout are known to seek out salmon spawning areas to take advantage of food subsidies (e.g., eggs and flesh; Bartlett and Hansen 2000).

We used an exponential logistic resource selection function (RSF; Lele and Keim 2006; Lele et al. 2012) to compare environmental conditions in used stream reaches (i.e., where Rainbow Trout were detected using radio telemetry and known to be present) with available

reaches drawn at random from the study area extent under 99 bootstrap iterations. The RSF models were constructed in Program R (R Development Core Team 2012) using the 'ResourceSelection' package (Lele 2009; Lele et al. 2014). The RSF approach uses random sampling of the used-available habitat database from a weighted distribution to generate a maximum likelihood estimate of the probability of use for each habitat factor (Lele 2009; Kowal et al. 2014; Gagné et al. 2015). Predictors were examined for collinearity based on the variance inflation factor (VIF). Covariates with VIF > 5 were not included in models (Montgomery et al. 2012).

We used an information-theoretic approach to select the best model predicting Rainbow Trout seasonal habitat selection, given the data (Burnham and Anderson 2002). Candidate models were built separately for each season, based on the following sets of predictors and based on the hypotheses presented above: overwintering (channel gradient, sinuosity, MAF), spawning (channel gradient, sinuosity, MAF, D50), early feeding (channel gradient, sinuosity, MAF), and late feeding (channel gradient, sinuosity, MAF, CHINIP). All possible combinations of variables were considered for each seasonal model. The top model for each season was selected based on Akaike's information criterion corrected for small sample size (AICc) scores; those with the lowest AICc were considered top models. Model fit for top models was assessed based on the Hosmer-Lemeshow goodness of fit (GOF) test (Hosmer and Lemeshow 2000). In order to address model uncertainty, we averaged parameter estimates over models with Akaike weights (w_i) ≥ 0.05 and reported the relative importance of each covariate included in the confidence model set (RI; Barton 2012).

RESULTS

Fish capture and tagging.—Thirty-seven adult Rainbow Trout were captured and tagged in 2003 during 12-13 angling days in each of the four tributaries (Total $N = 148$; Table 1.1) with an additional 45 and 39 fish tagged in Willow Creek in 2013 and 2014, respectively. The percentage of fish with hooking scars ranged from 10.8% in the Kashwitna River in 2003 to 71.8% in Willow Creek in 2014 (Table 1.1). Hooking scars were assumed to be caused by catch-and-release sport angling, and included deformity and laceration of the upper and lower jaws, operculum, and noticeable crossbite. Trout lengths were similar across tributaries and years

(mean FL = 483, SD = 56.4; Table 1.1). Information on post-tagging and annual mortality of tagged fish is presented in Appendix 1.A.

Genetic sex identification.—All but two Rainbow Trout from Willow Creek in 2013 and 2014 were successfully assigned to sex. DNA was denatured for one of the unknown fish, likely due to decomposition in a faulty storage vial, and the other trout was released before taking a fin clip in order to minimize additional stress after observing the fish was exhausted and sluggish post-surgery. Results of the analysis found that there were 16 males and 27 females tagged in 2013 and 12 males and 27 females in 2014.

Fish locations, seasonal movement, and tributary fidelity.— Twenty-one aerial telemetry surveys of the Susitna River basin were conducted during the study period ($N = 11$ in 2004; $N = 10$ in 2014). A total of 1,272 fish locations were recorded for trout that survived tagging and gave one or more live signals (Table 1.2). Trout were detected in the mainstem Susitna, Talkeetna, and Chulitna Rivers, and tributary drainages including Willow Creek, Little Willow Creek, Kashwitna River, Sheep Creek, Goose Creek, Montana Creek, and Chunilna Creek (Figure 1.1). Fidelity to stream of capture ranged from 33.3% in the Kashwitna River during the spawning season to 100% in Willow Creek in 2014 during the late feeding season (Table 1.2). Complex movements were observed in 9.5 - 11.7% of trout from Willow, Montana, and Chunilna Creeks, while 22.7% of the Kashwitna River fish exhibited these movements.

We found that Rainbow Trout moved long distances (up to 218.5 km – longest individual TAM), and those movements differed by season and tributary. Total annual movements were not significantly different among Rainbow Trout tagged in Willow, Montana, and Chunilna Creeks (Tukey's HSD; mean = 42 km, SE = 37.90, all $P > 0.62$), but trout tagged in the Kashwitna River traveled significantly farther (mean = 105.1 km, SE = 52.87, $P < 0.001$; Figure 1.5). The shortest annual movement observed was 4.5 km (2004 Montana Creek), whereas the longest was 218.5 km for a trout from the Kashwitna River. Similar to TAM, ISM was significantly different only for trout tagged in the Kashwitna River (mean = 28.5 km, SE = 19.73, $P = 0.006$) and did not differ for those tagged in other tributaries (mean = 16.5 km, SE = 18.30, all $P > 0.05$). Inter-seasonal movement was significantly different among all seasons (overwintering, spawning, early feeding, and late feeding) when pooled across tributaries (all $P < 0.03$; Figure 1.6a). Trout made the longest ISM's between overwintering and spawning seasons (mean = 28.5 km, SE = 18.53), and the shortest ISM distances were between early and late feeding season habitats (mean

= 8 km, SE = 13.56). Trout remained closer to their respective tributary confluences during the overwintering season (mean DFC = 1.8 km downstream, SE = 17.25) than during spawning (mean DFC = 19.0 km, SE = 18.1; Figure 1.6b). There was a significant interaction between tributary and season (ANOVA; $F = 2.52$, df = 12, $P = 0.003$), suggesting that fish from different tributaries show slightly different patterns in their orientation to the tributary confluence over seasons.

Willow Creek 2013-2014 sex bias.— Post-tagging mortality/tag rejection rates of 2013-2014 Willow Creek Rainbow Trout were higher for females (2013=65.4%, 2014=37%) than males (2013=37.5%, 2014=25%) in both years. Although no significant differences were found between sexes in mean TAM (ANOVA; $F = 0.13$, df = 1, $P = 0.73$, Figure 1.7), ISM ($F = 0.11$, df = 1, $P = 0.74$, Table 1.3), or DFC ($F = 0.01$, df = 1, $P = 0.93$, Table 1.3), there was a significant interaction between sex and season in DFC that indicates different sexes may exhibit slightly different orientations in relation to the tributary confluence, contingent on season ($F = 2.92$, df = 4, $P = 0.02$).

Habitat use.— Variance inflation factor values for all covariates were acceptable (VIF < 5). Across seasons, predicted values from each top model for Rainbow Trout resource selection closely fit the observed values (all Hosmer-Lemeshow GOF P –values < 0.05). The top models selected for overwintering Rainbow Trout resource selection (Table 1.4) suggested that the likelihood of trout overwinter habitat use increased with SINU and MAF, and decreased with GRAD (Table 1.5). The best-supported models for Rainbow Trout spawning habitat use indicated that trout habitat use was affected by SINU (+), D50 (+), GRAD (-), and MAF (+). However, unconditional confidence intervals for GRAD and MAF overlapped zero (Table 1.5). For the early feeding season, the top models of trout habitat selection included MAF (+), GRAD (-), and SINU (-) with confidence intervals for GRAD and SINU overlapping zero. Finally, the top models for the late feeding season included CHINIP (+), GRAD (+), SINU (+), and MAF (-). The confidence interval for MAF overlapped zero.

DISCUSSION

Our research showed that potamodromous Rainbow Trout within a complex, glacially influenced river basin moved long distances and occasionally utilized multiple tributaries within and among seasons. Inter-tributary movements suggest a basin-wide metapopulation and heterogeneity in

trout movements. Habitat use by trout varied across seasons, with individuals selecting stream reaches with characteristics supporting refuge from harsh overwinter conditions, spawning in the spring, and feeding over summer months. In general, individuals exhibited a novel seasonal movement pattern where they overwintered in glacially-influenced mainstem reaches during the long ice-covered season from October to May, moved into upper reaches of clearwater tributaries during the spawning season from mid-May to early June, and remained in tributaries to feed from mid-June through September. Movements varied among seasons, with the longest average distance traveled being from overwintering to spawning. Here we synthesize information from this study to describe seasonal movement and habitat use of potamodromous Rainbow Trout and discuss conservation and management implications of this ecologically and economically important species.

Seasonal habitat use and movements.— During the overwintering season (September through May) Rainbow Trout almost exclusively used mainstem Susitna and Talkeetna River habitats with lower gradient and higher sinuosity and mean annual flow. Exceptions to this include seven (22.6%) fish that were tagged in the Kashwitna River that remained within the tributary and five (17.9%) fish tagged in Chunilna Creek that overwintered in a stream-lake system within the tributary. However, these places likely provided refuge similar to mainstem habitats because the Kashwitna River was the largest of the tributaries with deeper habitats available, and lakes are known to be overwintering habitat for Rainbow Trout (Northcote 1997, Meka et al. 2003). Trout likely chose habitats with lower gradient and higher sinuosity and MAF because minimizing movement and choosing suitable habitat (optimal temperatures, high-volume reaches without bedfast ice; Brown and Mackay 1995) in order to conserve energy during the long, harsh overwintering season is critical to adult trout survival. Trout use of mainstem rather than tributary habitats in the Susitna River basin is similar to what has been observed in other salmonids (Jakober et al. 1998; Brown et al. 2001), and is likely tied to flow and temperature selection. About half of the tagged fish remained in close proximity (< 10 km; 54.9%) to the confluence of their tributary of capture, but a sizeable proportion (45.1%) moved longer distances up- or downstream along the mainstem rivers. This individual variation in movement may be due to density-dependent competition or random exploratory movements by highly-mobile individuals (e.g., staying allows a fish to be closer to spawning habitats, but closer habitats near tributary mouths may have an overabundance of competitors for resources; Gowan

et al. 1994; Skalski and Gilliam 2000; Radinger and Wolter 2014). Therefore, the likelihood for longer movements vs. remaining near the tributary mouth during the overwintering period likely differs between fish based on individual competitive ability (including prior residency).

During the spawning season (mid-May to early June), stream reaches predicted to have optimal spawning substrate size (15-25 mm), higher sinuosity and larger mean annual flows, and lower gradients were selected by Rainbow Trout. Substrate size is important for spawning salmonid habitat because the size of particles dictates the ability for dissolved oxygen to flow through interstitial space to embedded eggs and alevin and for waste (e.g., CO_2) to be carried away (Olsson and Persson 1988; Kondolf and Wolman 1993). Flow and gradient are likely important to Rainbow Trout year-round, as evidenced by the inclusion of these variables in the top RSF models for each season. Fish seek out areas with velocity that minimizes energy expenditure but adequately delivers drifting food items to juveniles and adults (Bisson et al. 1988; Cram et al. 2013). Tributary fidelity was lowest in all tributaries during the spawning season, suggesting inter-tributary mating and genetic mixing within the Susitna River basin metapopulation. Movements were longest between overwintering and spawning habitats (average ISM = 28.7 km), likely because habitat characteristics conducive to spawning were located in smaller tributaries having geomorphic attributes that promote adequate substrate size and upwelling for spawning which are located farther away from the mainstem.

Habitat selection during the early feeding season (pre-salmon arrival, mid-June to mid-July) included reaches with lower gradient and sinuosity, and higher flows. Flow was the only covariate with a confidence interval not overlapping zero, and as previously mentioned is likely important for trout during all seasons. The lack of strong habitat selection observed during this season is undoubtedly a result of a generalist feeding strategy that trout are known to employ post-spawning, where trout opportunistically feed on aquatic and terrestrial invertebrates, outmigrating juvenile salmon, and even small mammals (Scheuerell et al. 2007; Lisi et al. 2014). Relative to subsidies provided by spawning salmon, these food sources are not necessarily concentrated in particular stream reaches within a drainage, and so trout are distributed more widely and habitat use is more likely to be driven by intra-specific competition rather than physical habitat characteristics (Hughes 1998; Alanärä et al. 2001). Movements between spawning and early feeding were second shortest, on average (mean ISM = 14.7 km), indicating that spawning and feeding habitats were in closer proximity than spawning and overwintering

habitats. This may be due to fish attempting to conserve energy after engaging in energetically demanding spawning activity during the previous weeks.

During the late feeding season (post-salmon arrival, late July through early September), Rainbow Trout were more likely to select smaller, sinuous, high-gradient stream reaches with high Chinook salmon spawning habitat potential (IP). This was likely owing to the propensity for trout to concentrate near spawning salmon aggregations to gorge on drifting eggs and sloughed salmon flesh to maximize energy intake critical for overwinter survival (Bartlett and Hansen 2000). This phenomenon is also seen in Rainbow Trout and Dolly Varden char (*Salvelinus malma*) in other regions of Alaska, where observed diets have been comprised of up to 80-90% salmon eggs and flesh during this season (Eastman 1996; Scheuerell et al. 2007; Rinella et al. 2011). Salmon eggs are estimated to contain roughly 4,500 cal/g of wet weight (although the measure of this value is highly variable within and among species of salmon), which is approximately 15% higher than aquatic or terrestrial invertebrates (Eastman 1996, Armstrong 2010). Salmon flesh contains less energy than both eggs and invertebrate prey (only 645 cal/g wet weight; Eastman 1996), but it is abundant and easy to ingest. Interestingly, fidelity to tributary of capture was highest in most tributaries during the late feeding season, likely because of the high abundance of salmon-derived food. Fish were more likely to return to the tributary of capture to feed than to spawn, suggesting that feeding habitats within a tributary are highly abundant and not density-limited, whereas spawning habitats are less abundant and may be density-limited. During this season trout follow the food source of highest abundance and caloric content, and their habitat use is well-predicted by characteristics that describe high quality salmon spawning habitat potential (i.e., CHINIP).

Sex bias.— We found no evidence of sex-biased annual or inter-seasonal movements in the 2013-2014 Willow Creek Rainbow Trout sample, contrary to our hypothesis. However, there was a significant difference in abundance between males and females (65.9% female, 34.1% male overall; binomial test) with a female: male ratio of roughly 8:5 in 2013 and 11:5 in 2014. This female-dominated ratio is similar to that seen in anadromous Rainbow Trout/Steelhead populations along the West Coast of the U.S. (56-76% female, Ohms et al. 2013. In contrast, other literature documented male-dominated partially migratory Rainbow Trout populations in California and the Naknek and Gulkana Rivers of Alaska as well as in other salmonids such as migratory Dolly Varden char in Japan (Schwanke 2002; Fleming 2004; Koizumi et al. 2006;

Rundio et al. 2012). It is unclear why the sex ratio is biased towards females in the non-anadromous Susitna River basin population, but may suggest that males have higher mortality rates than females in early life stages since juvenile *O. mykiss* are thought to exhibit a 1:1 ratio (Ohms et al. 2013). Another possible explanation is perhaps a higher proportion of females are skipping spawning each year and the sex ratio is equal on the spawning grounds, or sampling methods were biased and females were more likely to be captured.

Assumptions.— We made several assumptions when interpreting the results of this research. First, we assumed that there was no major capture bias for adult trout tagged with radio transmitters with respect to sex. It is possible that more females were captured and tagged than males, either because fewer males may have reached sizes greater than 400 mm (minimum tagging size) due to mortality or differential growth or that females may have been more aggressive feeders, making them easier to catch. However, it is likely that the female-biased sample reflected the true population composition because habitat use and movement comparisons showed no difference between sexes, indicating behavior and likelihood of capture should be similar. In addition, males were more mobile (lower proportion of zero weekly movements; K. M. Fraley, unpublished data) during the late feeding season when the majority of fish were captured, so the likelihood of capturing a male should have been equal or greater to the likelihood of catching a female. Finally, a higher proportion of males (75%) exhibited hooking scars when compared to females (48%), indicating that females were likely not feeding more aggressively. We also assumed that the process of tagging (i.e., capture stress, surgery, and recovery) did not artificially alter habitat use and movements of trout beyond approximately three weeks from the tagging date. This assumption was based on estimated surgery recovery time (Summerfelt and Smith 1990; Jepsen et al. 2002; Bridger and Booth 2003), supported through snorkel observation of recently tagged fish and angler reports of recently-tagged fish feeding as soon as 3 days after release (K. Fraley, *personal observation*).

We also assumed that fish not detected in the lower Susitna River Basin during aerial surveys were dead and had drifted out of the study area rather than had survived but moved beyond the reach of our surveys (e.g., out to sea or up distant Susitna River basin tributaries that we did not survey; Appendix 1.A). It is possible that some of these missing fish moved into lakes or remote tributaries where they would have been missed by telemetry surveys, although less likely that they traveled to salt water. There has been no documentation of anadromous

forms of *O. mykiss* (Steelhead) in the Susitna River Basin, although sympatric non-anadromous Rainbow Trout and steelhead populations are common in other large river basins in the region (e.g., Kenai Peninsula, Kodiak Island, and Alaska Peninsula streams; Behnke 2002) and in other similar glacially influenced systems in Alaska (e.g., Copper River; Eaton and Adams 1995). Consequently, we considered emigration out of the drainage or into saltwater unlikely. It is also possible that mortality signals or disappearance of a transmitter from the study area was due to a rejection of the tag from the body of the host fish and not death (Ivasauskas et al. 2012).

We also assumed that trout did not undertake long movements at a temporal scale finer than among-season (i.e., daily or weekly). This assumption may be invalid during the open-water spawning and feeding seasons, considering Willow Creek fish moved an average of 1.76 km/week in 2014 (mixture of directed and undirected movements; K. M. Fraley, unpublished data), and if that is the case then metrics such as TAM and ISM may be slightly underestimated compared to true values. Also, we assumed that habitat variables (e.g., substrate size, CHINIP) derived from existing models and developed for different regions were applicable to the Susitna River basin. However, as these models were parameterized for rivers in the Pacific Northwest and are relatively coarse-scale, they are likely adequate for stream networks in Alaska, including the Susitna River basin. Finally, we assumed that fish captured in a tributary were born and remained in that tributary and were not transients from other drainages. This is likely a robust assumption, as out-of-tributary movements were observed at a fairly low prevalence during the tagging periods (i.e., late feeding season).

Implications.— Susitna Basin Rainbow Trout are an economically and ecologically important native sport fish in the Susitna River basin, and need to be managed carefully in order to maintain healthy populations. Results of this study show that Rainbow Trout use a wide variety of habitats throughout the Susitna River Basin during different seasons, and there is evidence for a basin-wide metapopulation (sensu Falke and Fausch 2010). A metapopulation typically consists of habitat patches that harbor local populations (i.e., tributaries), and dispersal and movement between these patches reduces the risk of extinction of any local population by allowing recolonization following disturbance events or years of no recruitment. The Kashwitna River subpopulation may be an important vector of gene flow in the basin owing to the prevalence of long-distance and out-of-tributary movements by trout from this drainage (average TAM, ISM, and DFC were significantly higher). Additionally, the propensity of Kashwitna

River trout to undertake movements away from their tributary of capture may indicate low-quality or limited availability of seasonal habitats in this drainage, potentially owing to the substantial glacial influence (turbidity) in this tributary. Higher turbidity may result in reduced sight distance for trout, lowering feeding efficiency and increasing the difficulty in locating conspecifics for mating, which may prompt movements to less-turbid tributaries. High tributary fidelity in Willow, Montana, and Chunilna Creeks suggests there is an abundance of quality seasonal habitats available for trout in these drainages.

As a result of possible metapopulation dynamics, it is critical to manage Rainbow Trout at a basin-wide scale and maintain riverscape connectivity in order to account for the migratory nature of these diverse subpopulations. The Alaska Department of Fish and Game Rainbow Trout management approach has evolved over the last several decades, with recent emphasis on conservative harvest limits and catch-and-release angling in order to promote healthy populations and trophy trout fisheries (Bartlett and Hansen 2000). This can be seen in the transition from a 10 fish per day bag limit in the 1980's to the designation of Willow and Montana Creeks as catch-and-release only and the prohibition of bait and treble hooks in other Susitna tributaries in 1997. Significant harvest of Rainbow Trout still occurs in the Susitna River basin, and the effect of heavy catch-and-release angling, as evidenced by the presence of hooking scars on about one-third of all captured fish, may increase stress, cause exhaustion, and result in higher risk of mortality (although fish with hooking scars in our study were not found to have significantly higher rates of mortality; Appendix 1.A). Additionally, the dependence of trout on salmon-derived food items to gain adequate energy to survive winter highlights the importance of maintaining healthy Susitna River salmon runs (Scheuerell et al. 2007). This is particularly important because a significant proportion of salmon populations are currently declining across Alaska and the Pacific Northwest region (Hilborn 2013). It will be important for managers to closely monitor Rainbow Trout and salmon population levels in the Susitna Basin into the future.

Another factor that may influence Rainbow Trout in the Susitna River basin is increased anthropogenic impacts in the region. Examples include the proposed Susitna-Watana Hydropower Project, human population expansion, road building, clearing of riparian vegetation, and fish passage issues (AEA 2013; MSBSHP 2013). Road building and riparian alteration could cause siltation and higher water temperatures in tributaries containing Rainbow Trout. This could be particularly harmful during spawning if siltation smothered eggs in redds or increased

temperatures caused deleterious changes in egg incubation and juvenile trout growth. The Susitna-Watana hydropower dam, currently in the planning and environmental assessment stage, would likely cause far-reaching effects in the Susitna River from dam operations that may include altered flow and thermal regimes and changes in turbidity, with effects on aquatic habitat in the mainstem Susitna River downstream of the site (Devil's Canyon in the middle Susitna River basin; AEA 2013; WDAFS 2015). The potential effects of this dam on salmon and non-anadromous fish populations (including Rainbow Trout) in the Susitna Basin are currently unknown but are the focus of significant research efforts. Baseline research from the current study that identifies and quantifies seasonal habitats of fish and wildlife potentially affected by development is important for before-after comparisons and monitoring. Overwintering habitat is of particular concern for Rainbow Trout downstream of the dam site because a high proportion of tagged fish from all tributaries used the mainstem Susitna River during this season. If winter base flows and water temperatures increase following dam construction, overwintering Rainbow Trout may be affected through increased energy expenditure from higher metabolisms. The Western Division of the American Fisheries Society penned a letter in 2015 opposing the construction of the Susitna Dam (WDAFS 2015), citing the oftentimes disastrous consequences of hydropower projects on fish populations in the contiguous United States and the dynamic glacial component of the Susitna Basin, which is far different than river systems where dams have been previously installed. In summary, potamodromous Rainbow Trout are an important ecological and recreational resource in freshwater systems of Alaska that need to be carefully conserved and managed, and declining salmon stocks, increased development, hydroelectric projects, and climate change threaten their populations.

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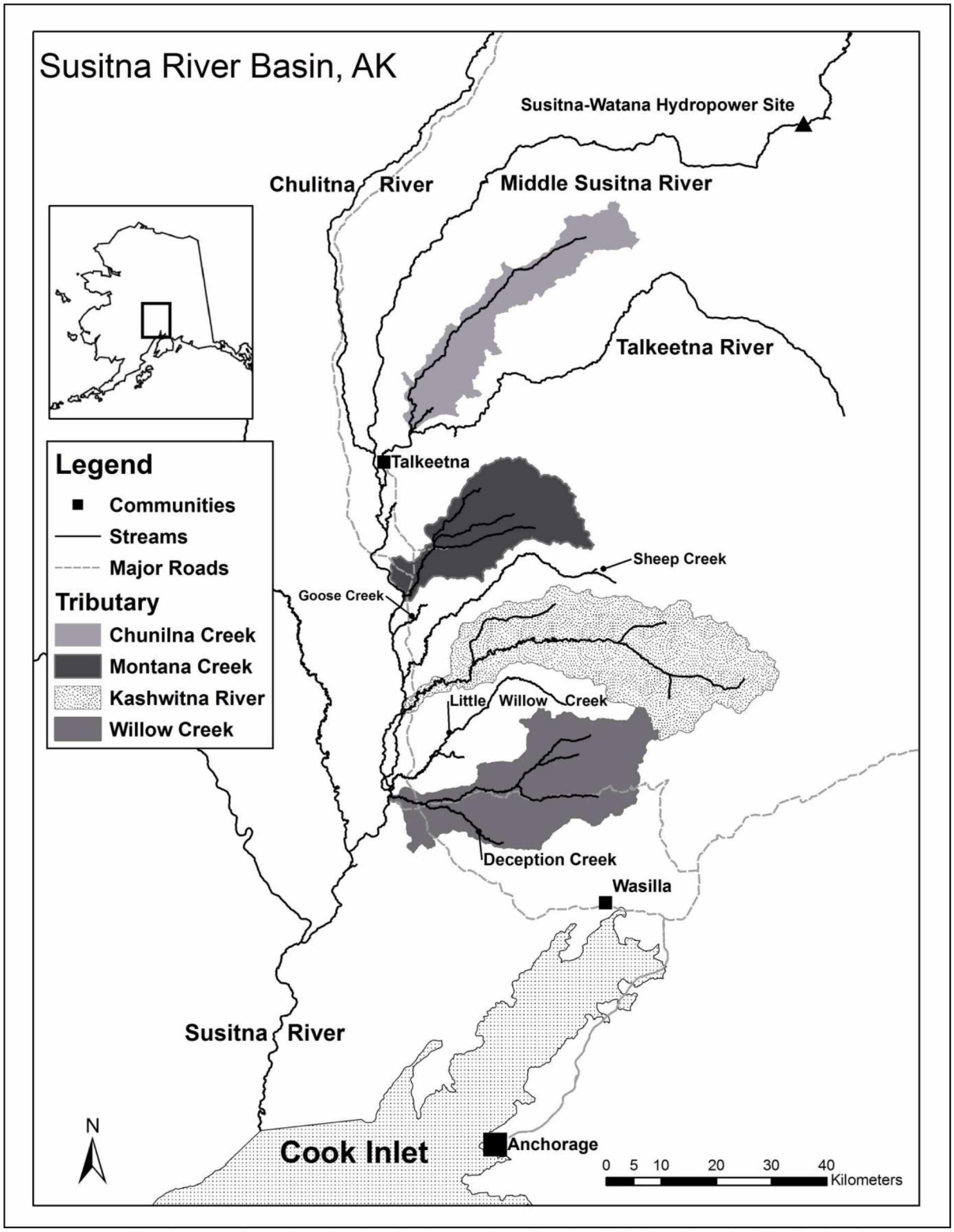

FIGURE 1.1. Study area location in the Susitna River basin, Alaska (inset). Shaded polygons denote tributaries where trout were tagged.

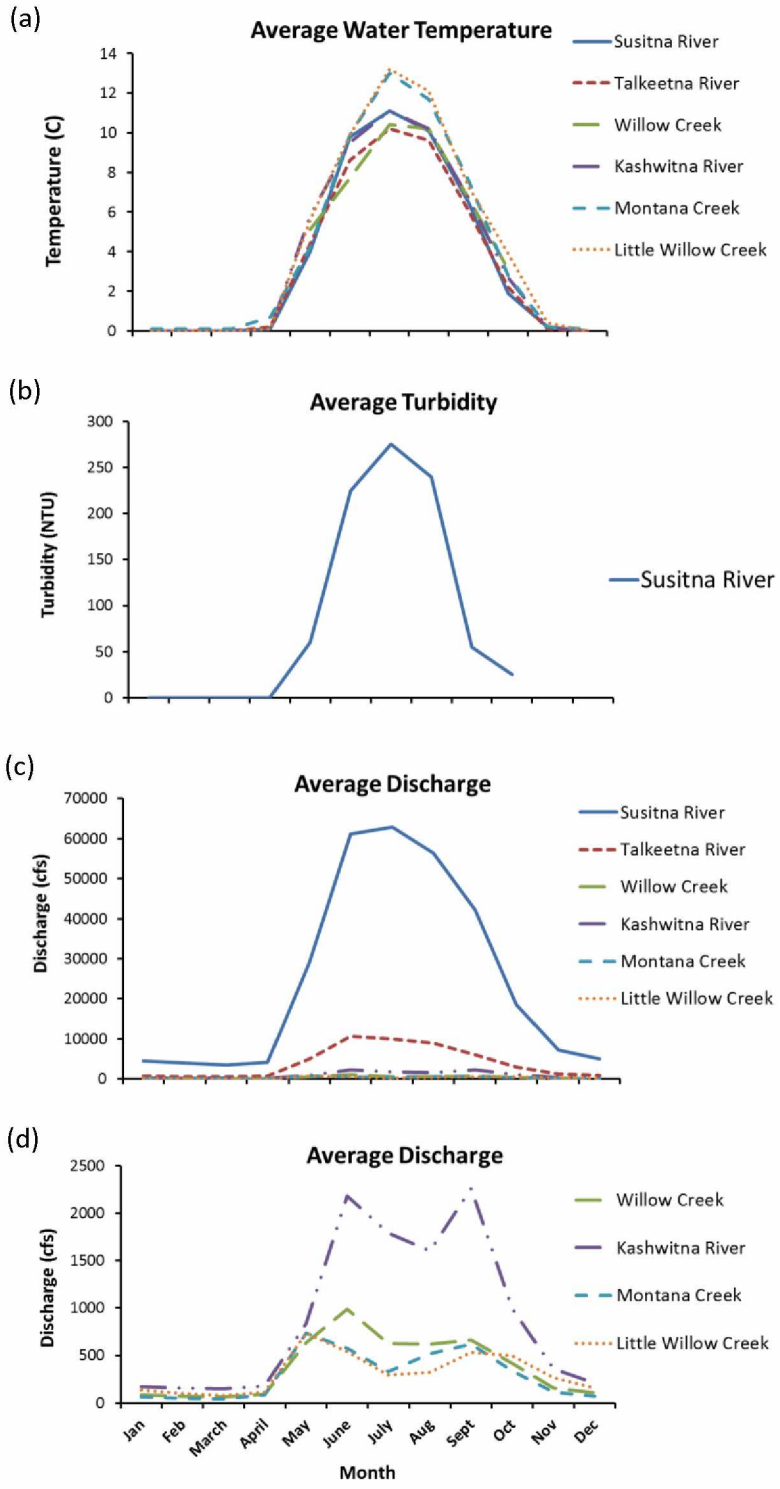

FIGURE 1.2. Mean monthly water temperature, turbidity, and discharge for the Susitna River, Alaska and selected tributaries from 1985-2014. Water temperature (a), average monthly turbidity for the Susitna River from 2011-2014 (b), average monthly discharge for mainstem rivers (c) and tributaries (d) from 1981-2014. Data were compiled from USGS streamgages in the region.

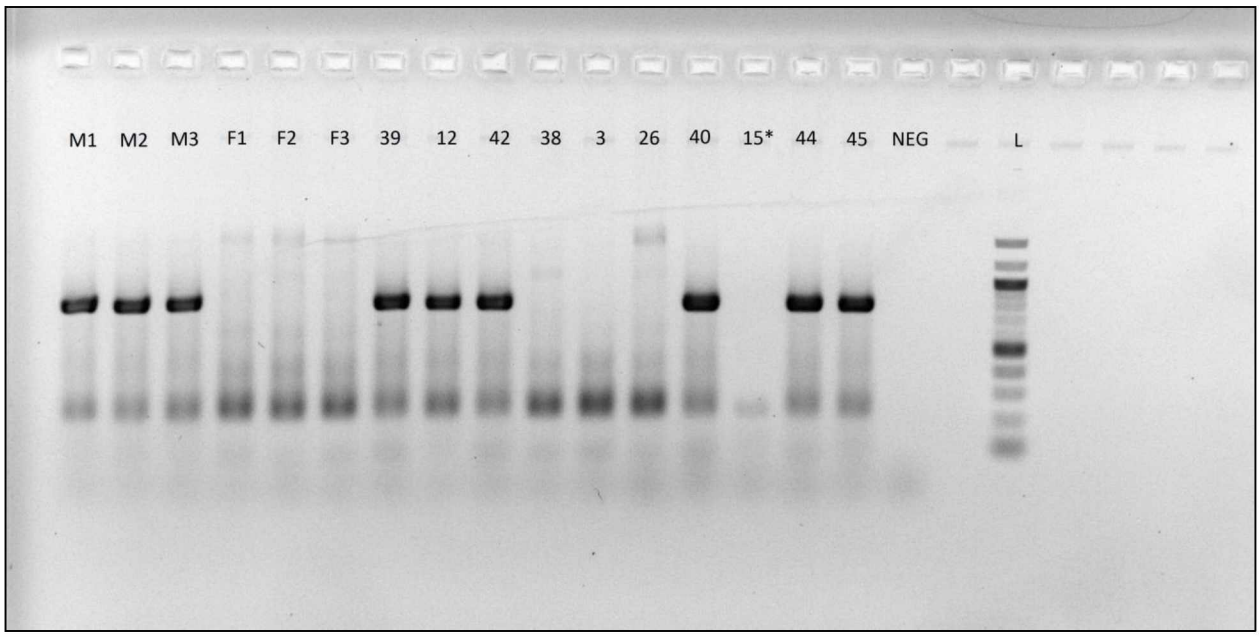

FIGURE 1.3. Example of an electrophoresis gel product used to determine sex of radio-tagged Rainbow Trout captured in Willow Creek, Alaska during 2013-2014. Fish ID numbers are listed at the top of the image. The black bands midway down each lane (792 bp) that are present for some fish but not for others identify the individual as a male. M1-M3 are known male controls, F1-F3 are known female controls. Fish ID's 39, 12, and 42 are example males and fish ID's 38, 3, and 26 are example females from the 2013 Willow Creek sample. Fish ID's 44 and 45 are random individuals being run repeatedly to ensure precision of the analysis, and Fish ID 15* is the individual that produced little or no DNA due to denaturing in storage. The lane labeled "NEG" denotes a negative control to ensure no contamination occurred, and "L" denotes a 100 base-pair ladder for reference.

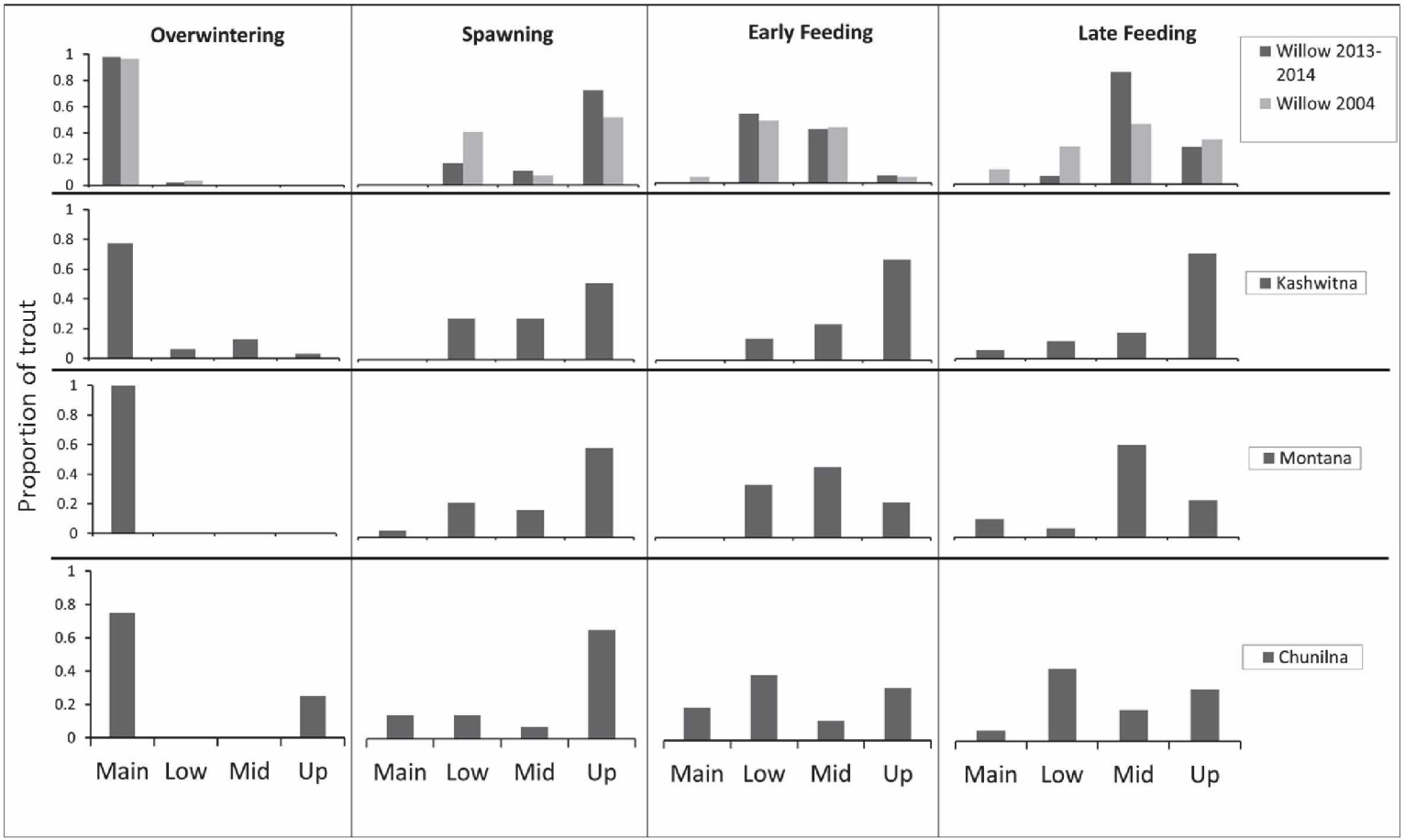

FIGURE 1.4. Trout locations characterized by longitudinal stream section by tributary and season. "Main"= Susitna, Talkeetna, or Chulitna Rivers. "Low"= tributary reaches below the Fairbanks-Anchorage Transmission Line for Willow Creek and Kashwitna River, below the East Fork on Montana Creek, and the lower 5.8 km of Chunilna Creek. "Mid"= tributary reaches between the Fairbanks-Anchorage Transmission Line and the Deneki Road bridge on Willow Creek, between the Fairbanks-Anchorage Transmission Line and the upper forks on the Kashwitna River , Between the East Fork and upper forks on Montana Creek, and between rkm 5.8 and the upper forks on Chunilna Creek. "Up"= all reaches upstream of the "Mid" reach on each tributary, as well as any forks off of the main channel. Sample sizes for each tributary, year, and season correspond to those listed in Table 1.2

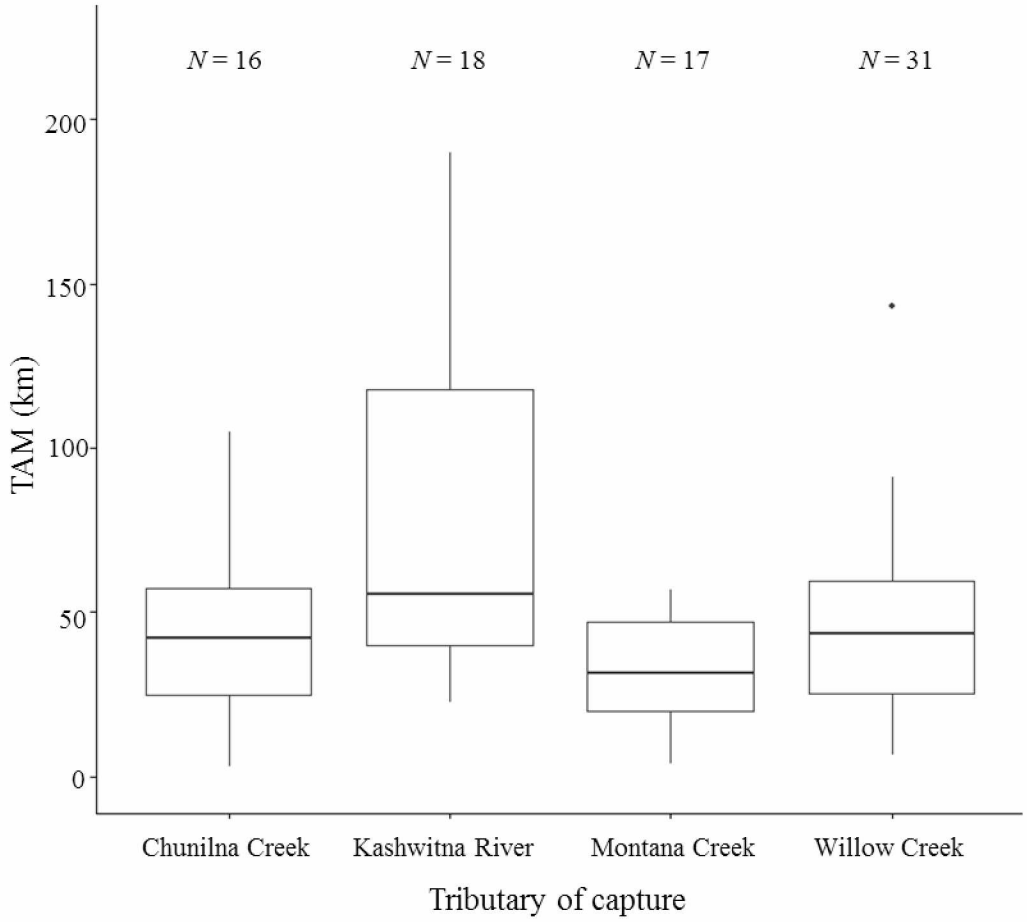

FIGURE 1.5. Total annual movement (TAM; km) of radio-tagged Rainbow Trout from the Susitna River basin, Alaska by tributary of capture. Boxes represent the 25th and 75th percentiles, whiskers the 10th and 90th percentiles, solid lines the median, and dots indicate outliers.

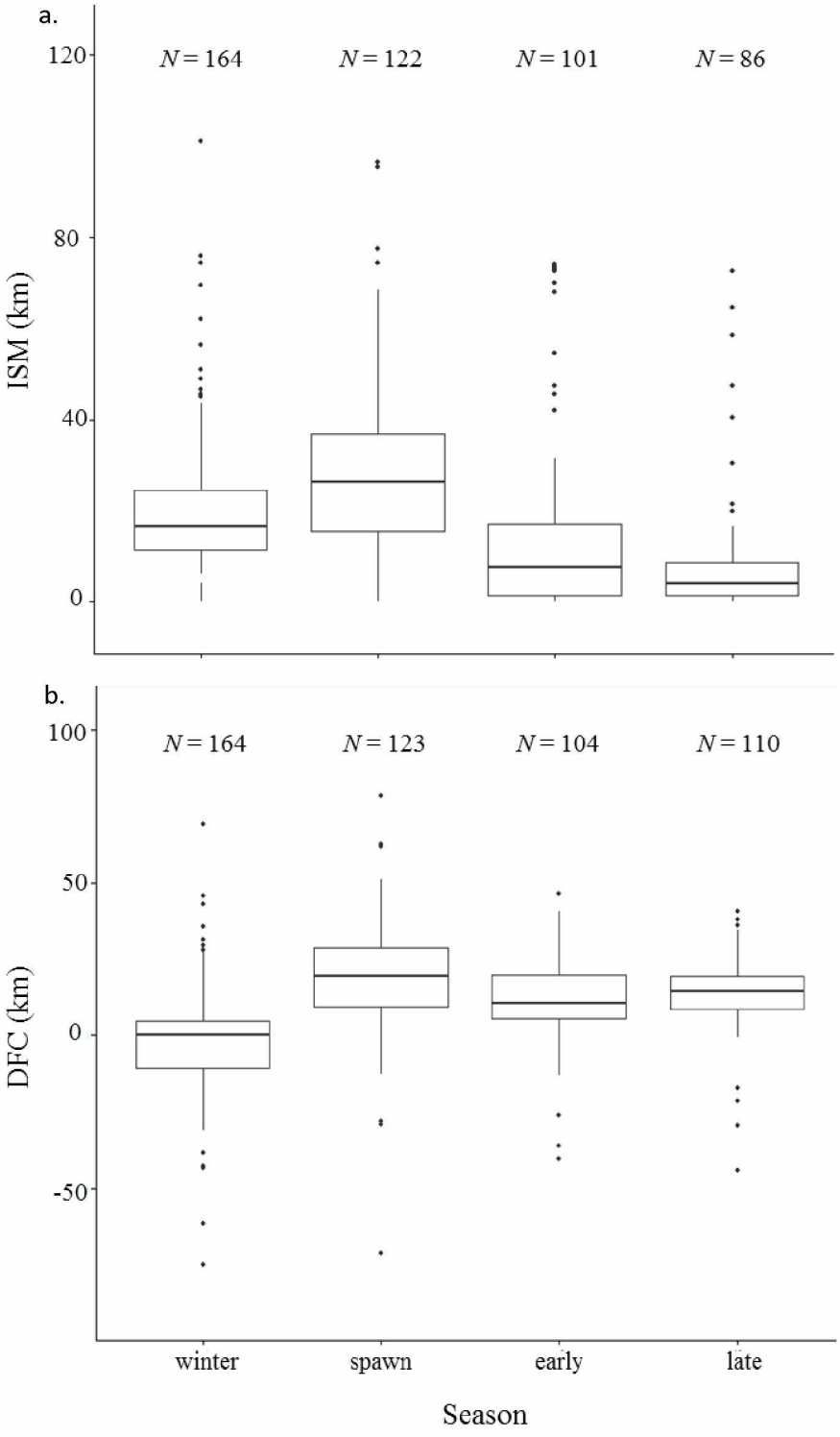

FIGURE 1.6. Inter-seasonal movement (ISM; km; a) and distance from tributary confluence (DFC; km; b) of radio-tagged Rainbow Trout from the Susitna River basin, Alaska among seasons, pooled over tributary of capture. Winter = overwintering season, spawn = spawning season, early = early feeding season, and late = late feeding season. Boxes represent the 25th and 75th percentiles, whiskers the 10th and 90th percentiles, solid lines the median, and dots indicate outliers.

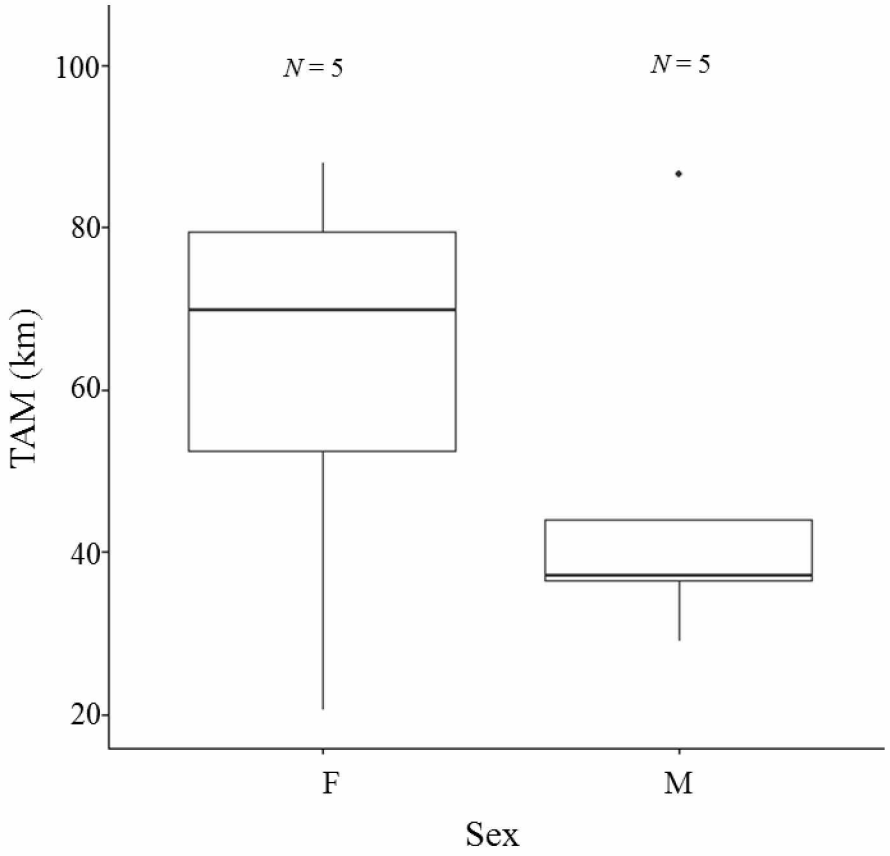

FIGURE 1.7. Total annual movement (TAM; km) by sex (M = males, F= females) of Rainbow Trout radio-tagged in 2013 and 2014 in Willow Creek, Alaska. Boxes represent the 25th and 75th percentiles, whiskers the 10th and 90th percentiles, solid lines the median, and dots indicate outliers.

TABLE 1.1. Summary of radio-tagged Rainbow Trout in the Susitna River basin, Alaska by tributary and year. The number of fish tagged, mean, minimum, maximum, and standard deviation of fork length (mm) percentage of fish with hooking scars (HS), and the number of fish that survived tagging and gave one or more live signals (Live) are shown.

			Fork length					
Year	Tributary	N	Mean	Min	Max	SD	HS	Live
2003	Kashwitna	37	476.05	407	648	53.73	10.8	31
2003	Montana	37	488.76	405	610	58.41	43.2	25
2003	Chunilna	37	492.70	408	670	60.07	13.5	28
2003	Willow	37	519.03	425	674	65.96	24.3	30
2013	Willow	45	459.82	401	545	38.44	42.2	21
2014	Willow	39	470.23	405	660	48.24	71.8	24

TABLE 1.2. Proportion of Rainbow Trout showing fidelity to tributary of capture, by tributary and year, with sample size in parentheses. Complex movements were defined as movements between multiple tributaries, or multiple seasons spent away from the tributary of capture. 'Willow 2013-2014' includes fish tagged in both years for all but the complex movements section, where only trout tagged in 2013 were included.

Tributary	Willow (2004)	Kashwitna	Montana	Chunilna	Willow (2013-2014)
Season					
Spawning	0.78 (27)	0.33 (27)	0.87 (23)	0.89 (28)	0.75 (20)
Early Feeding	0.81 (21)	0.68 (22)	0.89 (18)	0.96 (26)	0.94 (17)
Late Feeding	0.86 (21)	0.72 (18)	0.88 (17)	0.94 (16)	1.00 (38)
Complex Movements	0.10 (21)	0.23 (22)	0.11 (18)	0.12 (26)	0.12 (17)

TABLE 1.3. Mean, minimum, maximum, and standard deviation of distance of radio-tagged Rainbow Trout from the Willow Creek, Alaska confluence with the Susitna River (DFC; km) between sexes and seasons, and distance traveled from previous season's location (ISM; km).

		DFC (km)					ISM (km)				
Season	*Sex*	*Mean*	*N*	*Min*	*Max*	*SD*	*Mean*	*N*	*Min*	*Max*	*SD*
Overwinter	M	6.5 (20)	20	0.0	25.0	7.8	19.6 (21)	21	8.5	40.5	8.8
	F	5.8 (30)	30	0.0	29.5	9.4	22.6 (29)	29	11.0	49.0	10.5
Spawning	M	27.2 (10)	10	8.5	51.0	14.9	34.4 (10)	10	19.0	59.0	15.9
	F	18.3 (8)	8	4.5	32.0	9.0	22.4 (7)	7	6.5	46.0	14.0
Early Feeding	M	10.2 (8)	8	4.5	23.5	5.9	12.3 (7)	7	0.0	30.5	13.4
	F	9.4 (9)	9	1.5	16.0	4.3	16.3 (6)	6	0.0	45.5	17.4
Late Feeding	M	14.8 (13)	13	11.0	20.0	2.7	6.5 (5)	5	3.5	9.0	2.2
	F	16.9 (25)	25	11.0	23.0	3.2	8.8 (8)	8	1.0	16.5	5.4

TABLE 1.4. Summary of model selection statistics for top seasonal resource selection models for Rainbow Trout from the Susitna River basin, Alaska (Akaike weight [w_i] > 0.05). Abbreviations are as follows: L-L = the log-likelihood; ΔAIC_c= the difference in the corrected Akaike information criterion (AIC_c) value for a particular model compared with the top-ranked model; and K = the number of parameters, including the intercept and residual variance. Parameters are abbreviated as: GRAD = gradient (%); SINU = sinuosity; MAF = mean annual flow (m^3/s); D50 = median substrate size suitability for Rainbow Trout spawning; CHINIP = Chinook salmon spawning intrinsic potential.

Season	Model	L-L	AICc	ΔAICc	w_i	*K*
Overwinter	GRAD, SINU, MAF (global model)	-5905.33	11816.7	0.00	0.92	3
	GRAD, SINU	-5908.75	11821.5	4.83	0.08	2
Spawning	SINU, D50	-1920.09	3844.2	0.00	0.48	2
	SINU, D50, GRAD	-1919.83	3845.8	1.55	0.22	3
	SINU, D50, MAF	-1919.93	3846.0	1.75	0.20	3
	SINU, D50, GRAD, MAF (global model)	-1919.72	3847.6	3.41	0.09	4
Early feeding	GRAD, MAF	-1631.68	3267.4	0.00	0.53	2
	GRAD, MAF, SINU (global model)	-1631.66	3269.5	2.04	0.19	3
	MAF	-1633.72	3269.5	2.04	0.19	1
	MAF, SINU	-1633.67	3271.4	3.99	0.07	2
Late feeding	CHINIP, GRAD, SINU	-1417.9	2842.0	0.00	0.26	3
	CHINIP, GRAD	-1419.0	2842.2	0.16	0.24	2
	CHINIP, GRAD, MAF	-1418.7	2843.5	1.46	0.13	3
	CHINIP, GRAD, SINU, MAF (global model)	-1417.7	2843.6	1.58	0.12	4
	CHINIP	-1421.1	2844.3	2.27	0.08	1
	CHINIP, SINU	-1420.1	2844.3	2.28	0.08	2

TABLE 1.5. Model-averaged parameter estimates, relative variable importance (RI), and unconditional SE values and lower and upper 95% confidence limits (CLs) for covariates predicting seasonal resource selection of potamodromous Rainbow Trout in the Susitna River basin, Alaska. Estimates are derived from the confidence set of models with w_i>0.05 (Table 1.4).

Season	Covariate	Parameter estimate	Relative Importance	Lower 95% CL	Upper 95% CL
Overwinter	Gradient	-0.06 ± 0.03	1	-0.12	> -0.01
	Sinuosity	1.13 ± 0.08	1	0.99	1.26
	Mean annual flow	0.69 ± < 0.30	0.92	0.10	1.28
Spawning	Substrate	0.72 ± 0.15	1	0.43	1.01
	Sinuosity	0.84 ± 0.15	1	0.52	1.16
	Gradient	-0.02 ± 0.02	0.31	-0.07	0.02
	Mean annual flow	0.29 ± 0.56	0.29	-0.70	1.28
Early Feeding	Mean annual flow	1.31 ± 0.31	1	0.71	1.92
	Gradient	-0.08 ± 0.06	0.73	-0.19	0.03
	Sinuosity	-0.01 ± 0.28	0.27	-0.55	0.52
Late Feeding	Chinook IP	3.12 ± 0.73	1	1.64	4.60
	Gradient	0.11 ± 0.04	0.85	0.02	0.21
	Sinuosity	0.39 ± 0.19	0.43	< 0.01	0.78
	Mean annual flow	-0.50 ± 0.78	0.33	-1.91	0.91

APPENDIX

APPENDIX 1.A. Sources of mortality of radio-tagged Rainbow Trout.

Methods. —Logistic models explaining initial post-tagging mortality/tag expulsion were constructed in R (R Development Core Team 2012), with model covariates include tagging year (2003 and 2013-2014), fork length (mm), tributary (Chunilna Creek, Montana Creek, Kashwitna River, Willow Creek), and presence of hooking scars. AICc model selection was used to identify the top models (AICc weight >0.05; Table 1.A.1), and top models were averaged using the 'AICcmodavg' package to generate 95% confidence intervals for levels of each parameter (Table 1.A.2).

Results. —Cumulative mortality of telemetry-tagged fish was similar across tributaries of capture and between 2004 and 2014 samples (See Figure 1.A.1). Annual mortality could not be assessed for the Willow Creek sample tagged in 2014 because fish were not tracked for an entire year. Annual mortality ranged from 51% in the 2004 Kashwitna River trout to 75% in the 2013 Willow Creek fish. Initial post-tagging mortality/tag rejection was observed in 16.2% of the 2004 Kashwitna sample to 54.5% in the 2013 Willow Creek sample, and causation was analyzed for $N = 232$ trout from all tributaries and all years using logistic modeling (Table 1.A.1). Top models from AICc model selection (AICc weight >0.05) included 'year', 'tributary', 'hooking scars', and 'fork length' as potential predictors of initial mortality/tag rejection, however, only the 'year' covariate and the Chunilna Creek sample had 95% confidence intervals that didn't overlap zero in model averaging (Table 1.A.2). 'Year' was likely a significant factor in post-tag mortality/tag rejection because of a higher initial mortality rate in the 2013 Willow Creek sample, while it is unknown why Chunilna Creek fish had different initial mortality than other tributaries.

Discussion.—Annual cumulative mortality of Rainbow Trout tagged for this project (51-75%) was similar to other Rainbow Trout telemetry studies in Alaska. Other projects on the Gulkana River (Central Alaska), Alagnak River (Southwest Alaska), and the Aniak River (Western Alaska) found annual mortality from 35.1% to 71.2% (Fleming 2004; Meka et al. 2003; Schwanke 2002; Schwanke and Thalhauser 2011). In surgically implanted tagging studies it is difficult to identify sources of perceived mortality in the sample because fish are not visually observed. In the Susitna Basin, natural mortality likely accounted for a significant proportion of

trout total mortality, and may have included predation, starvation, senescence, harsh environmental conditions, and accidents. Predation was observed in dramatic fashion in Willow Creek when a 2013 tagged trout that was observed alive was tracked a week later to a bald eagle (*Haliaeetus leucocephalus*) nest ~1/2 km inland from Willow Creek. Additionally, the lack of food, long duration, harsh temperatures, and dynamic river ice conditions during the overwintering season in the mainstem Susitna and Talkeetna Rivers where trout were located may have contributed to annual mortality. Post-spawning deaths were also prevalent, particularly in Willow Creek in 2014 where 33.3% ($N = 12$) of fish that spawned died afterwards likely due to physically stressful redd-building, intrasexual competition, and redd defense during which trout typically do not feed.

Human harvest may also play a role in mortality in the Susitna River basin. Rainbow Trout angling is catch-and-release only in Montana Creek, Willow Creek, and the Kashwitna River above the Parks Highway Bridge. Other Susitna tributaries (including Kashwitna and Chunilna Creeks) allow harvest of 2 trout per day, although there is an annual limit of only 2 trout greater than 20 inches per angler. Both legal and illicit harvest of adult trout occurs. Legal harvest of Rainbow Trout in the Susitna River Basin averaged 2,032 fish per year from 2000-2010 (Jennings et al. 2011). Illegal harvest was reported by anglers in the Susitna River basin, and was observed firsthand by our crew in Willow Creek in 2014 (Angler killed and retained a trout >400 mm in our presence), although the prevalence and magnitude of this is unknown. Furthermore, a 2013 Willow Creek trout expired under circumstances that may have been an instance of illegal human harvest. One week after being confirmed alive in Little Willow Creek, the bare telemetry tag from the fish was found lying on a sandbar along Deception Creek, with only human footprints nearby (no trout carcass, bird, or bear activity in the vicinity). Finally, initial mortality (16-54%) contributed to total mortality, although it is unknown what proportion of post-surgery mortality was due to tag rejection or true mortality. Tag rejection, or the expulsion of a surgically implanted tag by the fish, has been documented previously, and a laboratory study found that tag expulsion occurred in up to 25% of internally tagged Rainbow Trout (Ivasauskas et al. 2012). Tag expulsion typically occurs 25-35 days after surgery, and trout that expelled tags exhibited a 100% survival rate in a lab study. Surgical procedure, surgical skill, and water temperature likely influence post-surgery mortality/tag rejection. The sample of fish tagged in 2013 in Willow Creek had higher post-tagging mortality compared to other years

and tributaries, likely due to warmer water temperatures causing higher stress in fish undergoing surgery, and the crew's burgeoning surgical aptitude. Post-tagging mortality/tag rejection was found to be different between tagging years and tributaries (Chunilna Creek had lower mortality than others), but fish fork length and the presence/absence of hooking scars was not different between fish that survived and those that expired.

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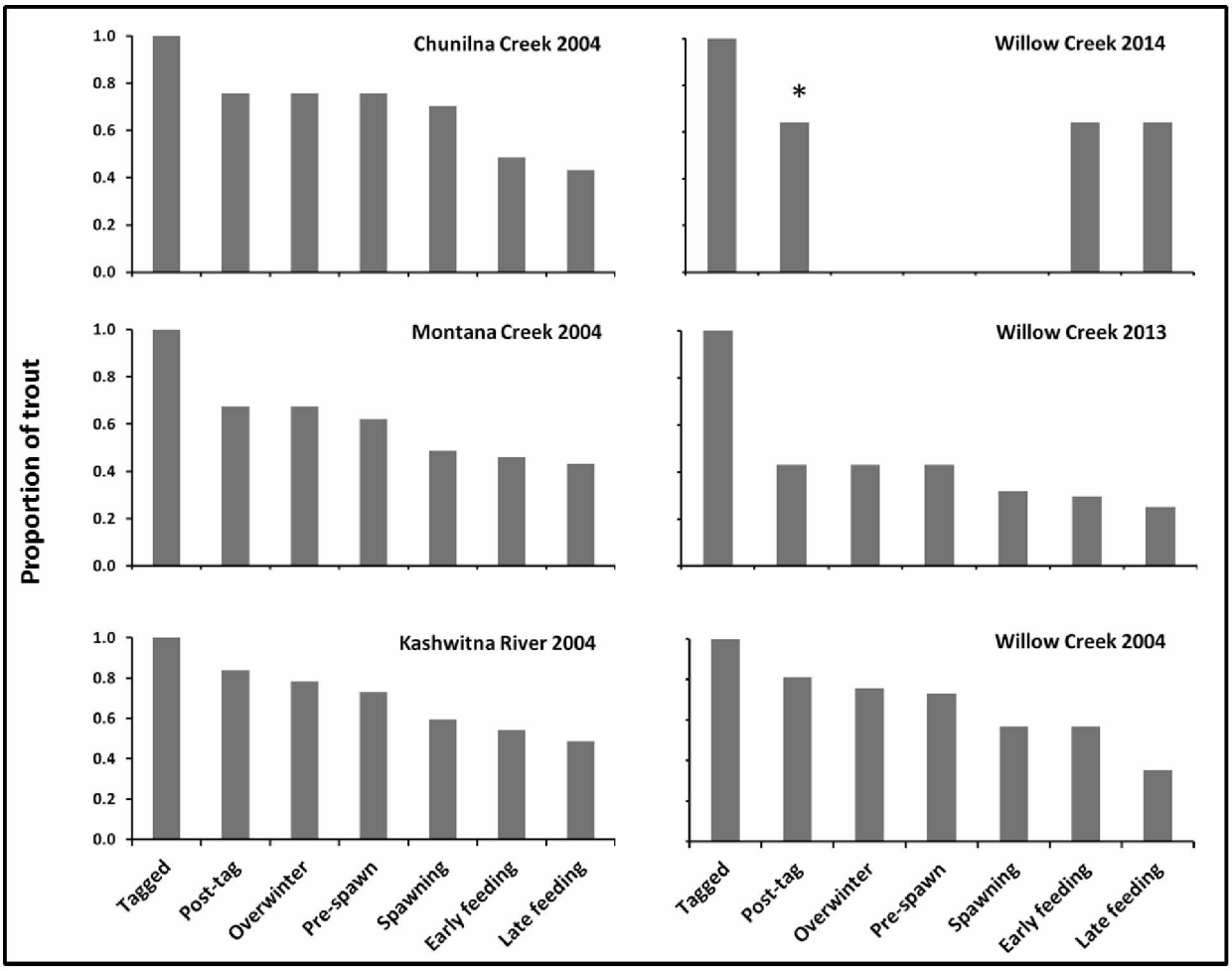

FIGURE 1.A.1. Annual survival of radio-tagged Rainbow Trout from Chunilna Creek 2004 (N = 37), Willow Creek 2014 (N = 39), Montana Creek 2004 (N = 37), Willow Creek 2013 (N = 44), Kashwitna River 2004 (N = 37), and Willow Creek 2004 (N = 37). * Trout were tagged in Willow Creek in 2014 during the early and late feeding seasons, thus mortality information for overwintering, pre-spawning, and spawning seasons is not available.

TABLE 1.A.1. Summary of logistic model selection statistics explaining initial post-tagging mortality/tag expulsion of Susitna River basin Rainbow Trout. Covariates include tagging year, fork length (mm), tributary (Chunilna Creek, Montana Creek, Kashwitna River, Willow Creek), and presence of hooking scars (Y or N). *N* = 232 trout were included in this analysis. Abbreviations are as follows: L-L = the log-likelihood; ΔAIC_c= the difference in the corrected Akaike information criterion (AIC_c) value for a particular model compared with the top-ranked model; K = the number of parameters, including the intercept and residual variance; and w_i = Akaike weight.

Model	L-L	AICc	ΔAIC	w_i	*K*
Year	-137.41	278.87	0.00	0.48	2
Year, hooking scars	-137.21	280.52	1.66	0.21	3
Year, fork length	-137.36	280.83	1.96	0.18	3
Year, tributary	-135.87	282.00	3.13	0.10	5
Year, tributary, hooking scars, fork length (global model)	-135.34	285.17	6.30	0.02	7
Tributary	-139.55	287.28	8.42	0.01	4
Tributary, fork length	-139.41	289.08	10.21	<0.01	5
Tributary, hooking scars	-139.54	289.34	10.47	<0.01	5
Hooking scars	-142.73	289.51	10.64	<0.01	*2*
Fork length	-142.75	289.55	10.68	<0.01	2
Hooking scars, fork length	-142.58	291.27	12.40	<0.01	3

TABLE 1.A.2. Standardized model-averaged parameter estimates, unconditional standard errors (SE), and 95% confidence limits (CLs) for covariates predicting initial post-tagging mortality/tag expulsion of Susitna River basin Rainbow Trout. Estimates are derived from the top models examined in Table A.1 with (w_i)>0.05 (year, tributary; global; year; and tributary models).

Covariate	Parameter estimate	SE	Lower 95% CL	Upper 95% CL
Year	0.10	0.03	0.04	0.16
Hooking scars	-0.20	0.33	-0.84	0.44
Fork length	0.00	0.00	-0.01	0.01
Chunilna Creek (Intercept)	-194.70	63.05	-318.28	-71.13
Montana Creek	0.40	0.52	-0.62	1.42
Kashwitna River	-0.51	0.59	-1.66	0.65
Willow Creek	-0.29	0.56	-1.39	0.81

Chapter 2: Weekly movements, fine-scale habitat use, and relationship with spawning Pacific salmon by rainbow trout in a southcentral Alaska river[1]

Abstract

We used field-measured and remotely-sensed aquatic habitat characteristics, weekly on-the-ground telemetry tracking, and occupancy models to describe movements, snorkeling detectability, and habitat use of adult potamodromous rainbow trout ($N = 82$) radio-tagged in 2014 throughout Willow and Deception Creeks, a runoff-fed southcentral Alaska river system. We found that during the ice-free feeding season (June through September) rainbow trout responded to fine-scale (channel unit) characteristics rather than more coarse-scale (stream reach) variables. The presence of Pacific salmon (which provide an important seasonal food subsidy), increasing mean water depth, and longer channel unit length were particularly useful positive predictors of habitat use. There was no evidence at the weekly and seasonal (pre and post spawning salmon arrival) temporal scales of sex-biased movements. However, weekly movements averaged over individuals were significantly longer (2.12 km) when spawning salmon were present compared to pre-arrival (1.12 km). Snorkel detectability of adult rainbow trout was high in clear water conditions, lower when fair, and zero when poor. The identity of the snorkel observer and the depth of the channel unit also influenced detectability.

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[1]Fraley, K.M., Falke, J.A, Prakash, A., McPhee, M.V. Rainbow trout fine-scale movements, Habitat use, and relationship with spawning Pacific salmon in a southcentral Alaska river. Formatted for submission to the Canadian Journal of Fisheries and Aquatic Sciences.

Introduction

Pacific salmon (*Oncorhynchus* spp.) provide important subsidies to freshwater and surrounding terrestrial ecosystems (Cederholm et al. 1999, Yang et al. 2008, Janetski et al. 2009). Adult salmon enter natal freshwater spawning systems in high numbers (sometimes millions of individuals) after a year or more of feeding at sea, and then spawn and die. During spawning, energy-rich salmon gametes are released in large quantities, some of which are not successfully deposited in the gravel and drift downstream. These gametes lack physical and chemical defenses, and are readily available to decomposers and predators such as fish, invertebrates, and shorebirds and are taken up as nutrients within the aquatic and adjacent terrestrial ecosystem (Janetski et al. 2009, Rinella et al. 2011). The importance of salmon-derived subsidies to non-anadromous salmonid movements and habitat use has not been well-studied, with the exception of Dolly Varden char (*Salvelinus malma*; Rinella et al. 2011) behavior and trophic-level relationships with rainbow trout (*Oncorhynchus mykiss*; Eastman 1996; Scheuerell et al. 2007) in Southwestern Alaska.

In non-anadromous stream salmonids, fine-scale (daily or weekly) movement patterns vary between species, populations, and life stages, with movements often triggered by environmental cues such as changes in flow, water temperature, or food abundance (Jakober et al. 1998; Hilderbrand and Kershner 2000; Brown et al. 2001). In stream fish populations it is common to observe a leptokurtic dispersal pattern where the majority of a population are more sedentary and only make short movements, while a smaller proportion of individuals are more mobile (Gowan et al. 1994; Skalski and Gilliam 2000; Radinger and Wolter 2014). Sedentary fish expend less energy but may miss out on abundant, localized food resources outside of their territory (Railsback et al. 1999). Fish that undertake frequent and lengthy movements expend more energy, but may be able to take advantage of higher-quality feeding areas, such as those with highest densities of spawning salmon. This risk vs. reward tradeoff has been predicted to drive dispersal processes in stream fishes, including anadromy in species with partially migratory populations (Kendall et al. 2014; McPhee et al. 2014). As a result, in salmon ecosystems observed variability in non-anadromous fish movements may be explained, in part, by the distribution and/or density of spawning salmon.

Habitat use and movement patterns within a species or population of fish may differ between sexes (Pusey 1987; Perrin and Mazalov 2000). In non-anadromous salmonids, females

may spend more time in feeding habitats where they exhibit risky behaviors to maximize energy input to gain reserves for the energetically demanding overwintering and spawning seasons (Appendix 2.A; Hutchings and Gerber 2002). Conversely, males may spend less time feeding, have larger home ranges, and undertake longer exploratory movements because less energy reserves are required for sperm production. In non-anadromous salmonids, a male-biased strategy is often observed where opportunistic males may range far and wide in search of food or mates (Hutchings and Gerber 2002; Olsen et al. 2006), although there are exceptions to this pattern (Koizumi et al. 2006). Movements of non-anadromous salmonids among watersheds where salmon-derived subsidies are available have been shown to vary among seasons and by sex (Northcote 1997; K.M. Fraley, unpublished data), but the relationship between sex and spawning salmon distribution has yet to be quantified.

Habitat use, occupancy, and abundance of stream fishes are often challenging to estimate given inherent variability in stream habitat conditions (e.g., water clarity, flow, temperature, etc.). Direct observation methods such as snorkel surveys are often employed to estimate occurrence and abundance of stream salmonids (Zubik and Fraley 1988; O'Neal 2007). These methods are useful because they do not harm fish or alter natural behavior, are fairly inexpensive, and personnel are easily trained to proficiency in the technique (Thurow 1994). However, inherent biases may confound the accuracy and consistency of this method, leading to spurious results (Rosenberger and Dunham 2005). Fish population estimates based on snorkeling may be biased owing to the observer if multiple observers are employed (i.e., different personnel may have varying proficiency; Orell et al. 2011), water clarity (e.g., fish are more likely to be observed in clear water; Zubik and Fraley 1988; Hillman et al. 1992), weather conditions (i.e., cloud cover or brightness of the sun affects likelihood of observing a fish; Thurow 1994), water temperature affecting fish activity (Hillman et al. 1992), and habitat complexity (e.g., more difficult to observe fish in areas with large woody debris; Wildman and Neumann 2003). Direct estimation of snorkeling detectability is rare for stream fish surveys (but see Orell et al. 2011) but important because unbiased estimates of species occurrence are important for evaluating and monitoring population vital rates, which in turn may have implications for conservation status and management. This is particularly true for rainbow trout in Alaska because of the dynamic environment characterized by rapidly changing flow conditions, turbidity from glacial influence,

natural habitat complexity (e.g., presence of LWD), and abundance of co-occurring spawning Pacific salmon (*Oncorhynchus* spp.).

Identification of the context within which critical habitats are determined, across broad landscapes, is an important tool to better monitor, manage, and conserve stream fish populations (Schlosser and Angermeier 1995, Wiens 2002, Naiman and Latterell 2005). Analysis of habitats at multiple spatial scales is essential because many species (e.g., potamodromous rainbow trout; Northcote 1997; K.M. Fraley, unpublished data) carry out their life histories across scales, and important habitat parameters may be excluded when focusing on only one level (Frissell et al. 1986, Schlosser 1991, Fausch et al. 2002). Combining spatially continuous habitat surveys taken at channel unit (10^0-10^1 m), reach (10^1-10^2 m), and watershed-scales (10^3-10^5 m) allows evaluation of the relative importance of these scales to predict the location of a target species and quantify how available habitats are used (Torgersen et al. 1999; Cram et al. 2013). The resulting fish-habitat relationships can be applied to other watersheds via resource selection modeling (Manly et al. 2002) to predict where important habitat occurs. Identification of critical habitats is particularly important for rainbow trout in Alaska in light of declining salmon populations in some areas, and increasing land development likely to impact trout and habitats via increased sedimentation, thinning of riparian zones, increased sportfishing pressure, altered flow and temperature regimes, and loss of habitat connectivity from installation of culverts and hydropower dams (AEA 2013; MSBSHP 2013).

Our overall goal was to gain a better understanding of how habitat utilization and movements of an Alaska population of native potamodromous rainbow trout during the open-water feeding season (June through September) relate to the presence of spawning salmon to provide information to better protect these economically and ecologically important fish. Our analyses were based on trout location, occupancy, and movement data collected through radio telemetry and snorkel surveys, characterization of multi-scale physical and biological characteristics of seasonal habitats surveyed in the field and calculated from a digital landscape model, and genetic sex identification of tagged fish. Our specific objectives were to quantify how rainbow trout movements and habitat use varied 1) before, during, and after the arrival of spawning salmon, 2) between sexes, and 3) across two spatial scales (channel unit and stream reach). We hypothesized that trout movements would decrease after the arrival of spawning salmon because of the spatially concentrated nature of salmon-derived subsidies (e.g., eggs and

sloughed flesh), and that males would undertake longer movements than females in search of feeding habitats owing to more flexible energy budgets. Finally, we predicted trout would select habitats at all spatial scales with high complexity for cover (large woody debris, sinuosity) and with spawning salmon present in order to capitalize on food subsidies.

Methods

Study area

Willow Creek is a clear-water, snowmelt runoff-fed stream with headwaters in the Hatcher Pass area of southcentral Alaska (Fig. 2.1). It flows into the turbid, glacial Susitna River near the town of Willow, Alaska, which drains into the upper Cook Inlet of the Gulf of Alaska. Willow Creek is home to substantial spawning runs of Chinook (*Oncorhynchus tshawytscha*), pink (*O. gorbuscha*), chum (*O. keta*), and coho salmon (*O. kisutch*, Hasbrouck and Edmundson 2007), as well as a large population of native non-anadromous rainbow trout. These salmon and trout are the targets of a popular sportfishery. Fishing for rainbow trout in Willow Creek is catch-and-release only, and trout are subjected to moderate pressure from fly fishermen during the summer months (June through September). Trout in the Susitna River basin rely heavily on salmon egg subsidies for food, and are dependent on healthy salmon spawning runs to gain sufficient energy reserves to survive the winter months (Bartlett and Hanson 2000). For this study we focused on the lower 18.5 km of Willow Creek from its confluence with the Susitna River to the lower end of the barrier canyon and the lower 11 km of Deception Creek (a major tributary to Willow Creek) from its confluence with Willow Creek to the Four-Mile Road area (Fig. 2.1). The Alaska Department of Fish and Game found during previous telemetry studies that the majority of rainbow trout remained within this 29.5 stream km study area during ice-free months (Yanusz 2009).

Channel unit habitat variables

Rainbow trout feeding season habitat use in the Willow and Deception Creeks study area (Fig. 2.1) was quantified at two spatial scales (channel unit - 10^0-10^1 m and stream reach - 10^1-10^3), similar to the approach suggested by Fausch et al. (2002) and using the hierarchical framework of Frissell et al. (1986). At the channel unit-scale, a spatially continuous physical stream habitat survey was conducted throughout the 29.5 km Willow and Deception Creeks study area (Table 2.1). All sampled channel units were visually classified as riffles, runs, or

pools (CLASS) and each type was further subcategorized (e.g., rapid, plunge pool, debris dam pool, scour pool, etc.; SUBCLASS) after Bisson et al. (1982) and Hawkins et al. (1993). Salmonids are known to select for pools, riffles, or runs depending on life stage, season, competitive ability, and energetic demands (Bisson et al. 1988; Hughes 1998; Walter 2012). Variables measured included maximum depth (cm; MAXD), wetted width (m; WW), and bankful width (m; BFW) which were measured along three equally-spaced lateral transects for each channel unit using a staff gauge and TruPulse laser rangefinder (Laser Technology, Inc., Centennial, Colorado, USA). Mean depth (cm; DEP) was calculated from measurements in three equidistant locations along each transect. Percent large woody debris cover (LWD), substrate type (SUB), and presence (SALM) and species richness (SALMR) of spawning salmon were visually assessed following methods outlined by Moore et al. (2002). LWD offers cover from predators and an abundance of invertebrate prey for salmonids (Fausch and Northcote 1992), substrate type can affect flow and habitat structure, and salmon can provide food subsidies (Scheuerell et al. 2007), so these variables are likely important for trout in Willow Creek. Stream gradient (%, cuGRAD) and channel unit length (m; LEN) were measured with the staff gauge and laser rangefinder. Stream gradient can serve as a barrier to upstream movements and influences streamflow velocity, which has implications for fish energy expenditure (i.e., swimming speed), and delivery of dissolved oxygen and food resources. Channel unit total volume (m^3; VOL) was calculated as the product of WW, LEN, and DEP. Channel unit dimensions are likely important for trout because these measurements capture the available area and physical characteristics of a habitat, which has implications for water temperature and metabolic rates, feeding territory size, predator avoidance, and carrying capacity (Dunham and Rieman 1999; Rahel and Nibbelink 1999). Habitat data for each channel unit were recorded using an Archer field computer with a Hemisphere XF101 GPS receiver (Juniper Systems, Logan, Utah, USA) and polylines representing the length of each channel unit were created and georeferenced using ArcPad 10.0.4 (ESRI, Redlands, California, USA).

Stream reach-scale habitat variables

Reach-scale habitat characteristics for the study area were derived from channel unit-scale measurements or attributes from a digital landscape model (NetMap; Benda et al. 2007; www.terrainworks.org) parameterized for the Matanuska-Susitna river basin (Table 2.1). The NetMap model generates an analytic digital stream network layer based on a remotely-sensed

digital elevation model (DEM) comprised of 50-200 m stream reaches (delineated based on properties including drainage area, channel gradient, and channel width) which are linked to the surrounding landscape and attributed with geomorphic characteristics (e.g., gradient, stream width, drainage area, etc.; Clarke et al. 2008; Bidlack et al. 2014). The Matanuska-Susitna River basin DEM was based on synthetic aperture radar (SAR; 5-m res) and light detection and ranging (LIDAR; <1-m res) imagery. We used NetMap instead of the National Hydrography Dataset (NHD) for the state of Alaska because the current Alaska NHD is low quality relative to data available for the contiguous U.S. (e.g., coarser scale, misrepresented flow lines, disconnected and omitted streams).

We chose four NetMap attributes to represent physical and biological factors potentially important to rainbow trout within and among early (pre-salmon arrival) and late (post-salmon arrival) feeding seasons. The first attribute, channel gradient (rchGRAD; %) was generated by NetMap based on the underlying DEM (Clarke et al. 2008). We predicted that gradient would be important for both early and late feeding seasons owing to the propensity for fish to seek areas of optimal flow, and concentrations of food during these seasons (Walter 2012; Cram et al. 2013).

The second attribute, sinuosity (SINU), is a unitless ratio of the magnitude of meandering of a stream across its floodplain. Sinuosity is calculated by dividing the stream channel path length between two points along the stream (i.e., in-stream distance) by the shortest path length between those points (i.e., Euclidean distance). The metric ranges from 1 (least sinuous) to infinity (most sinuous; Friend and Sinha 1993). Sinuosity was calculated in NetMap with a channel path length equal to 40 times the channel width based on the relationship between sinuosity and meander geometry (Rosgen 1994). Similar to gradient, sinuosity affects stream flow (Wirth et al. 2012) and is also correlated with higher aquatic habitat complexity and is indicative of a stream channel unaltered by human development (Fausch and Northcote 1992). Thus, sinuosity is likely important for rainbow trout habitat selection throughout the ice-free period, particularly during late feeding season when trout are likely seeking salmon spawning areas to take advantage of food subsidies.

We chose mean annual flow (MAF; m^3/s) as a relative measure of stream size (Clarke et al. 2008). This metric was calculated using NetMap based on an equation for southcentral Alaska (Brabets 1996):

$$MAF = 1.025 * A^{0.024} * P^{1.186},$$

where P is mean annual precipitation (mm) and A is upstream drainage area (km^2). Flow is likely important to rainbow trout across seasons as they seek out areas with velocity that minimizes energy expenditure but adequately delivers drifting food items to juveniles and adults (Bisson et al. 1988). Stream size is likely also important because salmonids are known to occupy larger stream reaches and avoid lower-order reaches to take advantage of additional cover from terrestrial and aerial predators (Walter 2012). Finally, in addition to the NetMap attributes we derived reach-scale covariates from channel unit-scale measurements that included the proportion of channel units within a reach where salmon were observed (SALMP) and the number of pools per reach (POOLS).

Fish capture and tagging

Adult rainbow trout (>400 mm FL) were captured in Willow Creek in 2013 and 2014 via fly-rod-and-reel angling methods. Capture efforts occurred in the late summer-early fall during both years and throughout the study area, but were concentrated on the most accessible lower-middle reaches of Willow Creek. Fish eligible for surgery were landed quickly with a net and immersed in an anesthetic bath until stage 3-4 anesthesia was attained (Summerfelt and Smith 1990). In 2013 clove oil was used, and in 2014 AQUI-S^{TM} 20E (AQUI-S New Zealand Ltd, Wellington, New Zealand) was employed per permit stipulations. Trout with visible injuries or those showing signs of lethargy and exhaustion were rejected as surgical candidates and immediately released. Anesthetized fish were measured for fork length (FL; mm) and a subset was weighed (grams). Fish were then placed ventral-side up in a moist neoprene-lined cradle for surgery. A crew member continuously delivered anesthetic and oxygenated water to the fish's gills with a turkey baster and monitored rapidity of gill movements and movement of the fish for the duration of the surgery. A separate crew member conducted the surgery, first making a small 2-cm incision 1-2 cm off the mid-ventral line about 3-4 cm anterior of the pelvic girdle with a scalpel sterilized in Betadyne solution. A grooved rod was then inserted into the incision and towards the posterior of the fish. Next, a hollow 16-gauge needle was inserted into the fish just behind the pelvic girdle, and directed along the grooved rod until the tip reached the incision (Ross and Kleiner 1982). The antenna wire of a radio transmitter (F1835C, 17x44 mm, 14 grams, battery life capacity 483 days; Advanced Telemetry Systems, Isanti, Minnesota, USA) was then threaded through the fish via the hollow needle, and a radio tag was inserted, bottom first, into the incision site while using the transmitter wire to help position the tag in the fish.

After the tag was inserted into the body cavity of the trout, the incision was closed with three to four 3-0 PDS™ monofilament absorbable sutures about 1/8 inch apart close the wound. After suturing, the wound was dried with sterile gauze and a few drops of Vetbond™ surgical glue were applied. Vetbond™ takes about 10 seconds to dry, at which time mucous from an adjacent area of the fish was smeared onto the wound to facilitate healing. After each trout recovered from surgery in an aerated basin of fresh river water, a right pelvic fin clip was taken for genetic sex identification, and a numbered Floy™ FD-94 T-bar anchor tag was implanted at the base of the dorsal fin as an external identifier. Fully-recovered fish were released into a pool or other low-velocity habitat near the site of capture. Surgical tools were sterilized in an iodine-povidine solution and rinsed with a saline solution between each surgery.

Fish tracking

Fish tracking occurred weekly from 13 May to 2 September 2014 via inflatable raft and on foot. Weekly tracking typically consisted of two floats: 14.7 km on Willow Creek from the canyon to the George Parks Highway bridge, and 15 km from the northern braided section to the confluence with the Susitna River. Additionally, one hike along 10.5 km of Deception Creek from Four-Mile Road to the Deception-Willow Creek confluence was conducted. An ATS model R4500C telemetry receiver attached to a Yagi antenna was used to pinpoint and record fish locations to be used for analysis. The transmitter identification number, latitude, longitude, signal strength, and presence/absence of a mortality code were recorded for all surveys. Trout were tracked to an individual channel unit (e.g., riffle, run, pool; see above), and exact locations were determined based on the highest signal strength reported by the telemetry receiver. Fish mortality was determined by either a mortality signal given off by an inactive radio transmitter (internal tag motion-sensor, triggered by 24 hours or more of inaction), or by failure to locate the fish after two or more surveys of the study area. Post-tagging (e.g., initial) mortality was assumed when a fish gave repeated mortality signals or permanently disappeared from the study area during the first two telemetry surveys after tagging. It is likely that the disappearance of a tagged fish was due to carcasses drifting downstream or removal of the trout from the study area after death (owing to natural mortality, predation, or human harvest). It is possible that mortality signals or disappearance of a transmitter from the study area was due to a rejection of the tag from the body of the host fish and not death (Ivasauskas et al. 2012).

Genetic sex identification

Pelvic fin clips were taken from each tagged trout and stored in 95% ethanol. DNA was isolated in the laboratory using a DNeasy Blood & Tissue Kit (Qiagen, Inc., Hilden, Germany) and electrophoresed to verify success of extraction. Genomic DNA was used as a template in PCR reactions using primers OmyY1 F (5'-GTTCATATGCCAGGCTCAAC-3') and OmyY1 R (5'-CGATTAGAAAGGCCTGCTTG-3') following methods of Brunelli et al. (2008). Primers targeting salmonid mitochondrial genome fragments were used as a DNA quality control. All PCR products were dyed and examined using agarose gel electrophoresis. The resulting bands (viewed under UV light) were examined to determine the sex of each fish. Samples exhibiting horizontal bands at 792 base pair length were designated as a male and those without bands at this location as female. Fin clips were also taken from three known female rainbow trout from the Alaska Department of Fish and Game's Ruth Burnett Sport Fish Hatchery in Fairbanks, Alaska and three male rainbow trout from the Montana Fish, Wildlife, and Parks' Murray Springs Trout Hatchery near Eureka, Montana to serve as controls and verify the accuracy of the sex identification analysis. Each sample was processed 2-3 times to ensure precision of the analysis.

Snorkel surveys

Snorkel surveys were conducted throughout the study area within channel units randomly selected from three sub-sections of Deception Creek (3.66 km each) and six subsections of Willow Creek (3.08 km each; Fig. 2.1) when flow conditions allowed. Three channel units were surveyed each week in each section (total channel units per week snorkeled = 27). If a channel unit was deemed to be too dangerous to snorkel (e.g., areas with rapids, overhanging cliffs, and LWD that might trap a person underwater) a substitute unit within the same section was chosen randomly. Snorkel surveys were conducted based on recommendations from Thurow (1994) and O'Neal (2007). The snorkel observer was chosen at the beginning of each day by a coin toss, and entered the water at the upstream end of each channel unit and drifted downstream through the entirety of the unit. Multiple passes were made in wide, deep, or complex channel units where visibility was limited. Data recorded during each survey included counts of rainbow trout with and without tags, snorkel observer identity, water clarity (poor, fair, or clear), weather (overcast, partly cloudy, or sunny), stream water temperature (C°), and counts of salmon and other fish species present. Adult rainbow trout were those deemed to be > 400 mm (visually

estimated), tagged fish were those exhibiting a Floy tag and/or ventral antenna wire, and untagged fish did not clearly exhibit a Floy tag or antenna wire. Water clarity was denoted as 'poor' if visibility was less than ~ 1 m, 'fair' if >1 m but substrate was obscured, and clear if there was no impediment to vision. Weather was considered 'overcast' during rainy and low-light conditions, 'partly cloudy' when some cloud cover was present but not direct sunlight, and sunny if there was direct and unobstructed sunlight striking the water. Temperature was measured before each snorkel survey using a PRO 20 meter (YSI, Inc., Yellow Springs, Ohio, USA).

In addition to snorkel surveys to determine the presence of rainbow trout, we quantified trout detectability at a subset of sites using a blind snorkel observer approach. For this method, the (randomly assigned) telemetry operator located a radio-tagged fish in a channel unit and deployed a snorkeler without prior knowledge of trout presence to survey the channel unit. The first three channel units in each section with tagged trout present were sampled for detectability each week. Snorkeling and habitat methods during detectability surveys were the same as described above.

Fish locations and movement

Rainbow trout locations were imported into a geographic information system (GIS) using ArcMap 10.1 (ESRI, Redlands, California, USA) and snapped to the nearest field-measured channel unit polyline. Weekly movements of individual fish (WM; km) were measured in ArcMap. Total feeding season distance traveled (TD; km) was calculated by summing WM for fish that were tracked for five to fourteen weeks, excluding movements to and from spawning areas. We acknowledge that TD may be biased because movements were summed over differing lengths of time (due to mortality and tracking logistics), but still believe that this metric has descriptive merit. Movements during the spawning season (determined by visual and snorkel observation to end the week of May 27, 2014; K. Fraley, *personal observation*) were excluded from this analysis because many individuals spawned outside of the Willow and Deception Creeks study area in headwaters or other tributaries and were not able to be tracked from the ground. However, rainbow trout spawning dynamics and mortality information is presented in Appendix 2.A. Feeding season was determined to end at the waning of spawning salmon activity and beginning of ice-up after the week of September 3, 2014. For analysis of WM, the

feeding season was split into pre-spawning salmon arrival (early; 2 June to 2 July) and post-spawning salmon arrival (late; 7 July to 2 September).

Data analysis

Body condition indices (relative weight, *Wr*; Fulton's condition factor, *K*) were calculated for a subset of rainbow trout that were weighed in 2013. Relative weight is an assumed measure of a fish's body condition and overall health, and is calculated using the equation W/*Ws* *100 where W is the weight of an individual fish (grams) and *Ws* is the 'standard weight' of a fish of a given length, derived for rainbow trout in Simpkins and Hubert (1996) . Fulton's condition factor is a similar metric, and is calculated by the equation $K = 100*W/FL^3$, where FL is fork length (mm). Condition was compared using ANOVA between trout caught before and after peak spawning salmon abundance to determine the potential effect salmon-derived food subsidies had on trout body condition (and therefore energy storage). The peak salmon spawning date was estimated to be August 15, 2013 (K. Fraley, *personal observation)*.

We compared rainbow trout TD among sexes using analysis of variance (ANOVA). To address the potential for bias induced by non-normality and non-independence of data we compared results of the ANOVA with those of a randomized permutation test (Manly 2006) based on the same main effects. Results of the permutation test were identical to the ANOVA. Based on those results, we felt justified that proceeding with the simple ANOVA analysis would not substantially influence the interpretation of our results. We compared Rainbow Trout WM among early and late feeding seasons and sexes using two-way ANOVA, with WM averaged over individual trout to meet the assumptions of ANOVA and eliminate effects of observations on the same individuals over time (i.e., pseudoreplication). All ANOVA analyses were conducted in Program R version 3.1.3 (R Development Core Team 2012).

Rainbow trout snorkeling detection probability was estimated using logistic regression. A binomial response variable was created for adult rainbow trout (1 = detected, 0 = undetected) for surveys where a known telemetry-tagged trout was present in the channel unit. From snorkel surveys, detection covariates included were three categorical and one continuous descriptor: water clarity (WAT), weather (WEATH), and snorkel observer (OBS), and water temperature (TEMP; Baxter and Hagen 2010, Orell et al. 2011). From channel unit habitat measurements, maximum depth (DEPTH) and percent LWD (LWD) were included as possible predictors. Candidate models explaining detection probability for adult rainbow trout including all variable

combinations were evaluated using the generalized linear model (glm) function in Program R. The top models (AICc $w_i > 0.05$) were used to calculate model-averaged estimates for detectability covariates.

We evaluated the relationship between the presence of rainbow trout (channel unit scale) determined via snorkeling surveys and habitat characteristics, spawning salmon presence, and species richness measured at the channel unit (averaged to reach-scale) and reach levels during the early feeding and late feeding seasons (SEASON). Covariates were derived from channel unit measurements and reach-scale NetMap attributes (Table 2.1) calculated continuously across the Willow and Deception Creeks study area. Channel units were assigned to a NetMap reach based on their location. Multicollinearity of variables was investigated by calculating variance inflation factors (VIF; cutoff ≥ 5), and a set of generalized linear models was constructed with a binomial ('used/unused') response (Manly et al. 2002). Candidate models for habitat use were built using a two-step approach. First, the best set of habitat fixed effects was determined for each scale (i.e., channel unit or stream-reach). Next, a set of models was developed to address previously outlined hypotheses (i.e., possible influence of season, salmon presence, physical habitat attributes, etc.) at the two different scales separately and together.

We used an information-theoretic approach to select the best model predicting rainbow trout habitat selection, given the data (Burnham and Anderson 2002). The top model was selected based on Akaike's information criterion corrected for small sample size (AICc) scores; those with the lowest AICc and highest Akaike model weight (w_i) were considered top models. We averaged parameter estimates over models with AICc $w_i > 0.05$ to address model uncertainty.

Results

Habitat characteristics

We measured 48 km of stream, including multiple channels and off-channel areas and consisting of 854 channel units, for habitat characteristics (Table 2.1) along Willow and Deception Creeks during the summers of 2013 and 2014. The proportion of channel units classified as pools, riffles, or runs were similar between the two creeks (pool = 32.6%, riffle = 31.9%, run = 35.5%). Dominant substrate ranged from boulders near the mouth of the Willow Creek canyon located at the upstream end of the study area, to sand at the downstream end near

the confluence with the Susitna River. The most common type of substrate was gravel, followed by sand, then cobble. Silt was dominant in only five channel units and bedrock only observed in two. Mean wetted width was 15.5 m (SD = 9.0) and mean bankful width was 30.2 m (SD = 20.4). Mean depth was 39.0 cm (SD = 16.6), and maximum depth had a mean of 112.0 cm (SD = 56.0). Mean channel unit length was 56.5 m (SD = 54.5), channel unit volume had a mean of 264.5 m^3 (SD = 541.3), and mean stream gradient was 0.9% (SD = 1.0). Mean LWD percent coverage was 27% (SD = 23), and Pacific salmon spp. were observed in 32.8% of channel units surveyed. Reach-scale mean annual flow averaged 6.6 m^3/s (SD = 5.8), and sinuosity had a mean of 1.5 (SD = 0.4).

Fish capture and tagging

Forty-five surgery-sized trout were captured and tagged in Willow Creek in 2013 during 21 tagging days from 7 August to 29 September, with one fish mortality during surgery. Additionally, 47 undersized rainbow trout were captured and released. In 2014, 39 adult rainbow trout were captured in Willow Creek over approximately 12 tagging days from 17 June to 20 August (Total $N = 84$; Table 2.2). Trout lengths were similar across years (mean FL = 464.7, SD = 43.3; Table 2.2). Most fish were caught above the Parks Highway Bridge on Willow Creek near aggregations of spawning Chinook and chum salmon. More trout were captured in pool habitats in 2013 (49%; Table 2.2), while more were caught in riffles in 2014 (46%).

Genetic sex identification

All but two rainbow trout from Willow Creek in 2013 and 2014 were successfully assigned to sex (See Fig. 1.3 for an example of sex identification final electrophoresis gel). DNA was denatured for one of the unknown fish, likely due to desiccation and decomposition in a faulty storage vial, and the other trout was released before taking a fin clip in order to minimize additional stress after observing the fish was exhausted and sluggish post-surgery. The female: male ratio was roughly 8:5 in 2013 ($N = 16$ males and $N = 27$ females) and 11: 5 ($N = 12$ males and $N = 27$ females) in 2014.

Snorkel surveys

A total of 182 snorkel surveys were conducted in 2014. Blind surveys (telemetry-tagged fish present) made up 54 of these total surveys, whereas random channel unit surveys (no telemetry-tagged fish present) accounted for the remaining 128. All snorkel surveys undertaken

in 'poor' water clarity conditions returned zero counts of adult rainbow trout, so these surveys were not included in detectability analyses.

Top models (AICc $w_i > 0.05$) for trout detectability included maximum depth, water clarity, temperature, observer, and LWD as predictors (Table 2.3). However, considerable uncertainty existed in models with 90th percentile unconditional confidence intervals overlapping zero for all parameters with the exception of maximum depth (+), Observer 2 (-), and fair water clarity (-; Table 2.4). In other words, snorkeling detectability was higher in deeper habitats with clear water conditions as surveyed by Observer 1. Overall snorkel survey trout detection probability was 0.83 when water was clear and 0.68 when water was fair when all other predictors were held constant at average values (Fig. 2.2).

Fish movements

Total distance traveled for Willow Creek rainbow trout during the open-water feeding season ranged from 0 to 30.07 km, with a mean of 12.32 km (SD = 7.84) and was not significantly different between sexes (ANOVA, $p = 0.31$; Fig. 2.3). Weekly movements ranged from 0 to 15 km, and averaged 1.76 km/week (SD = 3.01; Fig. 2.4). Weekly movements averaged over individual trout (to eliminate pseudoreplication) were not significantly different between sexes (ANOVA, $p = 0.57$), but were significantly shorter during the early feeding (mean = 1.12 km, SD = 0.95) season compared to the late feeding season (mean = 2.12 km, SD = 1.48, $p = 0.02$; Fig. 2.5). There was no evidence of an interaction between sex and season for WM averaged over individuals ($p = 0.74$). During the early feeding season, a higher proportion of male trout (100% had one or more instances of zero WM) were less mobile when compared to females (87.5% had a zero WM). However, during the late feeding season a higher percentage of males were mobile (50% had a zero WM) in contrast to females (82.6% had a zero WM).

Habitat use

High variance inflation factor values (VIF > 10) for several NetMap reach-scale habitat variables (e.g., stream width, depth, and surface area) resulted in the removal of these variables from consideration in the model, leaving only MAF, SINU, SALMP, and POOLS. VIF was acceptable for all channel unit-scale variables. Model selection results of rainbow trout habitat use identified four top models (AICc $w_i > 0.05$; Table 2.5) that included a combination of channel unit and reach-scale habitat characteristics and the presence and diversity of spawning

salmon. Channel unit variables included were DEP, LEN, WW, VOL, SALM, and SALMR. Top reach-scale predictors included MAF and SALMP. A variable incorporating season (early and late feeding) was also included in the top models. Model-averaging of top variables (Table 2.6) indicated that trout selected longer, deeper habitats where salmon were present. Trout were present in fewer channel-units in the early season than the late season (43% vs. 44%, respectively), although this may not be biologically significant. Increased salmon richness was selected against. Unconditional ninety-percent confidence intervals (Table 2.6) indicated that parameters for all other predictors overlapped zero.

Body condition

Mean relative weight was 81.62 pre-peak salmon abundance and 103.89 after maximum abundance. Mean Fulton's condition factor pre-peak was 1.11, and increased to 1.39 after spawning salmon were at their highest abundance. Mean condition factor and relative weight were significantly higher after the peak salmon spawning period (ANOVA, $p < 0.01$; Table 2.7).

Discussion

This research shows that rainbow trout exhibit differential habitat selection over multiple spatial scales and respond to the presence of spawning Pacific salmon by altering habitat use and movements. In the case of Willow Creek rainbow trout, fish responded to finer-scale (channel unit) characteristics relative to coarse-scale (stream reach) variables. Habitat dimensions (e.g., length, depth, volume), along with the presence of spawning salmon were particularly useful positive predictors of habitat use, while trout selected against habitats with increased salmon richness. There was no evidence at either the weekly or seasonal (early and late feeding) temporal scales of sex-biased movements. However, weekly movements averaged over individuals were significantly longer during the late feeding season when spawning salmon were present. The proportion of females deemed less mobile was high across both early and late feeding seasons, while males were more sedentary pre-salmon arrival and equally split between sedentary and mobile strategies in the late feeding season. Snorkel detectability of adult rainbow trout was high in clear water conditions, lower when fair, and zero when poor. The identity of the snorkel observer also influenced detectability, and fish were more likely to be detected in deeper channel units (likely because of reduced habitat complexity).

Snorkel detectability

Similar to the results of other studies, snorkel survey detectability of telemetry-tagged rainbow trout in Willow Creek was most influenced by water clarity (Zubik and Fraley 1988; Hillman et al. 1992). In 'poor' water clarity conditions detectability was zero, detectability under 'fair' conditions was good (0.68), and 'clear' conditions allowed for the highest detection probability (0.83). Water clarity varies within and between streams, and over time, so accounting for detection bias when comparing snorkel data from streams or reaches with different clarities is important. Based on our results, rainbow trout snorkel surveys would not be feasible in water bodies with fair-poor water clarity (e.g., those with high glacial influence such as the Kenai River of Alaska or the Dean River of British Columbia). Also, the identity of the snorkeler significantly influenced rainbow trout detectability. This highlights the importance of standardizing personnel training and snorkel protocols if there are multiple snorkelers collecting the same data (Orell et al. 2011). If varying snorkeler proficiency is not accounted for, results may be biased. Interestingly, we found that detectability increased in deeper channel units. This is likely due to a generally higher abundance of adult trout in deeper habitats (>1.5 m) within the study area (making it more likely to spot at least one fish), and because the maximum recorded depth in Willow and Deception Creeks (3.4 m) is relatively shallow (the riverbed is clearly visible). Thus, the effect of depth may not be linear, with asymptotes in detection probability at a certain depth greater than that seen in the study area. Detectability was also influenced by temperature and LWD similar to findings of Hillman et al. (1992) and Wildman and Neumann (2003), although model-averaging found that these predictors overlapped zero and are thus marginally influential to detectability. In many Alaska streams, including Willow Creek, high abundances of salmon (i.e., hundreds or thousands of pink or sockeye (*O. nerka*) salmon in a single channel unit) during spawning periods could negatively affect detectability of other fish species such as rainbow trout. We conducted snorkel surveys in too few channel units ($N = 9$) with significant numbers of pink salmon (5 or more individuals; K.M. Fraley, unpublished data) to properly analyze the effect on snorkel detectability, but trout were only detected in two of these surveys (and only a single trout was detected in each), thus providing support for this idea.

Movements

Mean WM across both seasons was fairly low overall (~1-2 km/week), suggesting that habitats and food resources are relatively abundant and high-quality throughout Willow Creek

and over time. Contrary to our hypothesis that trout would move less per week during the late feeding season (post-salmon arrival) compared to the early season, mean weekly movements were longer during the late season. This may be due to increased intra-specific competition for concentrated food resources (produced by localized spawning salmon aggregations; Hughes 1992; Keeley 2001; Nordwall et al. 2001) or agonistic encounters with defensive salmon adults during the late season (Eastman 1996), causing trout to seek out other areas. Alternatively, early feeding season WM may be lower owing to the propensity for trout to remain sedentary in order to recuperate from the preceding spawning season, which is energetically costly (Appendix 2.A; Bry 1985). Several tagged individuals in Willow Creek were observed to have skin and fin erosion and lesions immediately after spawning in 2014, and two individuals died on the spawning grounds, likely due to the high cost associated with competing for mates and guarding redds (aerial surveys and snorkel surveys, K. Fraley, *personal observation*). For example, a male trout that was observed through underwater video to have significant physical damage after spawning moved downstream and remained in the same pool for 4 weeks, only leaving this location upon the arrival of spawning salmon. Thus, the high cost of spawning may result in a recuperation period during the early feeding season where individuals are mostly sedentary.

No significant differences in movements (WM or TD) were found between sexes, indicating that male and female rainbow trout exhibit similar strategies during the open-water feeding season. However, the proportion of male trout that had one or more WM of zero distance (deemed more sedentary) was higher than in females during the early feeding season, but lower than females (more mobile) in the late season. Male rainbow trout may be more sedentary post-spawning because they have been found to resume feeding slower than females after exposure to a stressful event (1-2 weeks; Pottinger and Carrucj 2000; Øverli et al. 2006).

Habitat use

Rainbow trout habitat use models with channel unit covariates ranked higher than those with reach-scale variables, but there was considerable model uncertainty (parameter estimates overlapping zero) indicating that reach-scale habitat characteristics were also potentially important. These findings highlight the importance of a multi-scale approach to fish habitat use, because responses to or relationships with a habitat characteristic that are significant at a certain scale may be overlooked at other scales (Frissell et al. 1986, Schlosser 1991, Fausch et al. 2002). If we had only examined reach-scale variables we would have overlooked the potentially

important channel-unit predictors of rainbow trout habitat use. Contrary to our hypotheses, LWD was not selected for by trout, possibly because cover is more important for juvenile rather than adult trout. However, presence of salmon was correlated with trout habitat use, which follows our hypothesis that trout would select areas where salmon were likely spawning to take advantage of egg and flesh food subsidies. Increasing mean depth and reach length were also selected for by fish, which is likely due to the propensity for trout to seek out deeper areas with cooler temperatures and sufficient cover from predators and available space to establish feeding territories (Baigun et al. 2000; Elliot 2000). This may also be due to the fact that larger habitats innately have a higher carrying capacity for trout, therefore the likelihood for observing one may be higher (Laliberte et al. 2014). Interestingly, increasing salmon richness was a significant negative predictor of habitat use. This may be due to increasing agonistic encounters with multiple salmon species, particularly with aggressive and abundant chum and pink salmon. Pink and particularly chum salmon have a kype with overdeveloped teeth that can inflict significant damage on fish that infringe upon their spawning territory (Keenleyside and Dupuis 1988; Tiffan et al. 2005). Additionally, salmon aggressiveness is density dependent, so salmon in areas of high abundance and richness would be the most defensive (Quinn 1999). Thus trout may avoid areas of high salmon abundance (and also richness) as observed by Eastman (1996). This may not be true for sub-adult rainbow trout because their small size may allow them to go undetected when salmon intraspecific competition is fierce; we were unable to analyze the movements of smaller rainbow trout due to limitations of radio-tagging smaller fish.

Assumptions

We made several assumptions when interpreting the results of this research. First, we assumed that there was no major capture bias for adult trout tagged with radiotransmitters with respect to sex. It is possible that more females were captured and tagged than males because fewer males reach sizes greater than 400 mm (minimum tagging size), or that females are generally more aggressive and feed more often (i.e., are easier to catch). We also assumed that the process of tagging (i.e., capture stress, surgery, and recovery) did not artificially alter habitat use and movements of trout beyond approximately three weeks from the tagging date. This assumption was based on estimated surgery recovery time (Summerfelt and Smith 1990; Jepsen et al. 2002; Bridger and Booth 2003), and was supported for our study by snorkel observations

and angler reports of recently tagged fish feeding as soon as 3 days after release (K. Fraley, *personal observation*).

In addition, it was assumed that weekly telemetry surveys were exhaustive and trout were not missed if they remained in the study area. It is possible that trout were not detected in the Willow and Deception Creeks study area, but unlikely as on-the-ground surveys were complemented by aerial surveys in May, June, and September 2014. These aerial surveys had a longer detection range (up to 3.2 km) and would have detected any fish located in a habitat within the study area not surveyed during weekly tracking (e.g., off-channel habitat, connected lake, or upstream of the study area bounds).

Implications

Similar to conclusions of other research (K. M. Fraley, unpublished data) spawning salmon presence and salmon-derived food subsidies in streams where both trout and salmon occur influence habitat use and movements for potamodromous rainbow trout during the feeding season. Habitat use models not including SALM were never included in the top set, but neither was the model with only SALM. This indicates the dual importance of spawning salmon and physical habitat characteristics for trout habitat selection. Trout likely rely on high-calorie salmon-derived food items to gain fat and energy reserves in order to survive the winter months and support gonadal development the following spring (Scheuerell et al. 2007; Armstrong and Bond 2013). This was observed in a subset of tagged fish in Willow Creek in 2013 that showed a significant increase in body condition factor after the arrival of spawning salmon (Table 2.7). Thus, the abundance of salmon-derived food items (and also adult salmon) has implications on trout fitness (survival, reproductive success) and river carrying capacity (total food availability, invertebrate secondary production) for rainbow trout (Denton et al. 2009; Rinella et al. 2011). Because of the potential importance of spawning salmon to rainbow trout population health, it is important that salmon are not overharvested and are kept at population levels high enough to avoid detrimental effects on non-anadromous salmonids (Eastman 1996, Scheuerell et al. 2007, Denton et al. 2009). However, a significant proportion of salmon populations are currently declining across Alaska and the Pacific Northwest region (Hilborn 2013). In order to foster ecologically and economically important trout populations while still allowing for a reasonable commercial catch of salmon, resource users from all backgrounds must make equal compromises to ensure the preservation of healthy salmon populations (Eastman 1996, Denton et al. 2009). This may include decreased

salmon and trout quotas and bag limits for commercial and sport fishermen and the utilization of substitute food items for subsistence users during times of low salmon abundance. In addition, protection of salmon spawning and freshwater rearing habitats in Alaska will be important in light of future climate change and human development such as urbanization and installation of hydropower dams, which may have cascading effects on salmon (and also trout) freshwater habitats (Prowse et al. 2006; Schick 2006; AEA 2013; MSBSHP 2013). Moving into the future it will also be important to regularly monitor salmon and trout abundance and habitat use at multiple spatial scales to identify and address potential threats (Fausch et al. 2002).

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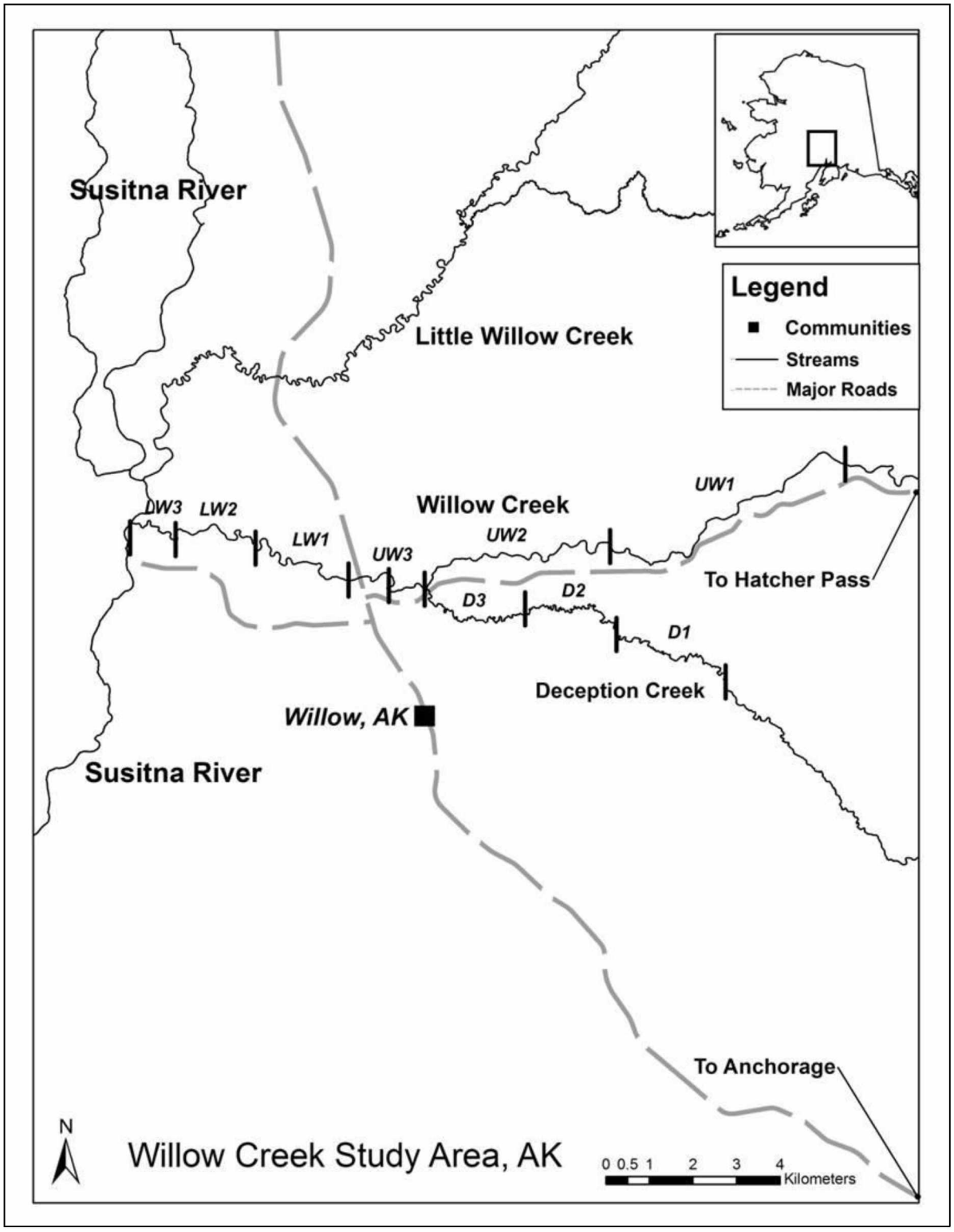

Fig. 2.1. Map of the study area in southcentral Alaska, USA. The location of Willow and Deception Creeks and nine snorkel survey sections are shown. ***UW*** = Upper Willow Creek, ***LW*** = Lower Willow Creek, and ***D*** = Deception Creek.

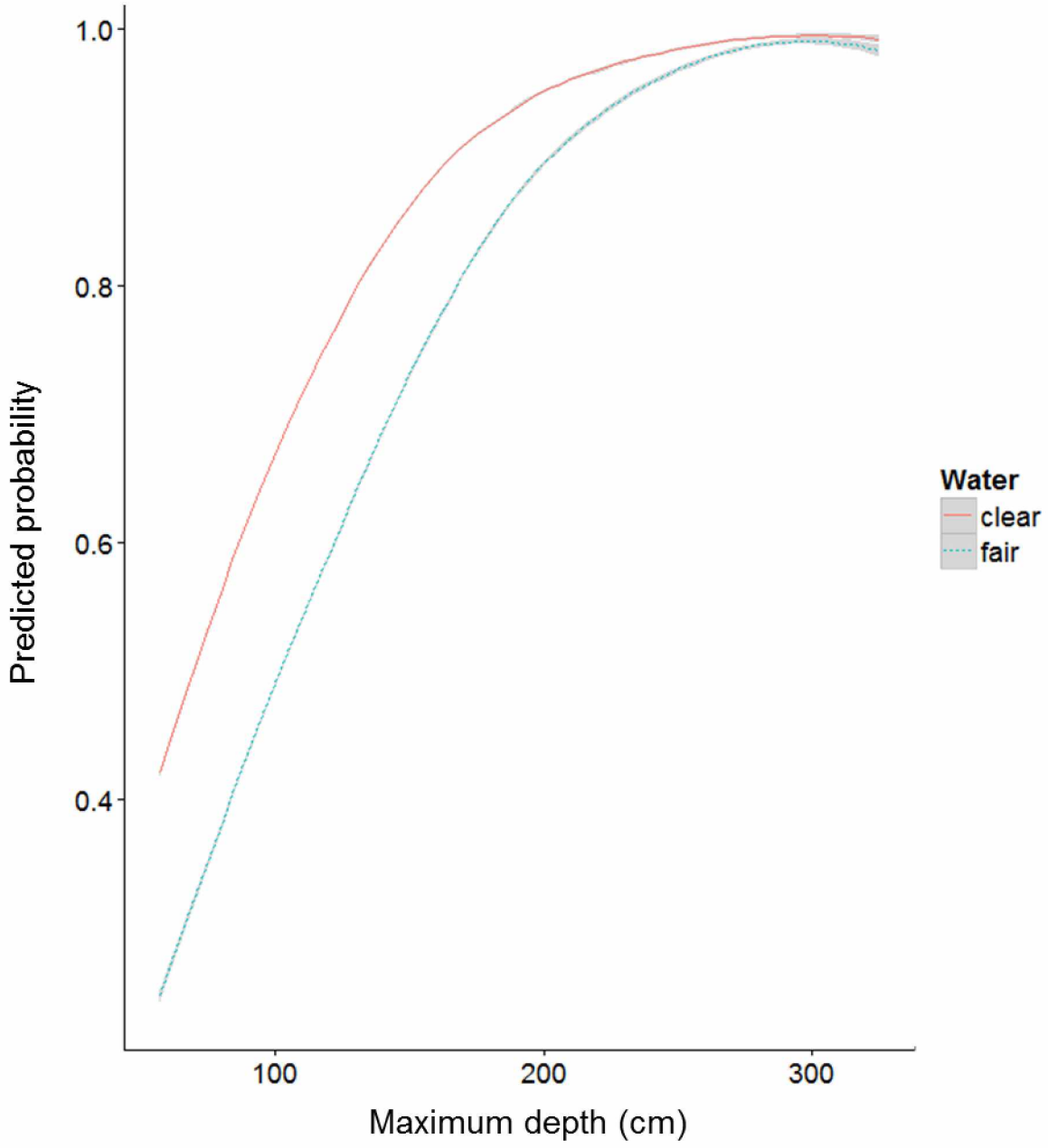

Fig. 2.2. Predictions from a model of snorkel survey detectability for adult rainbow trout in Willow and Deception Creeks, Alaska. Detection probability (y-axis) versus maximum depth (cm; x-axis) is shown for clear (red line) and fair (blue dashed line) water clarity conditions. Other covariates included in the model (observer, water temperature, and percent LWD) were held at average values for these predictions.

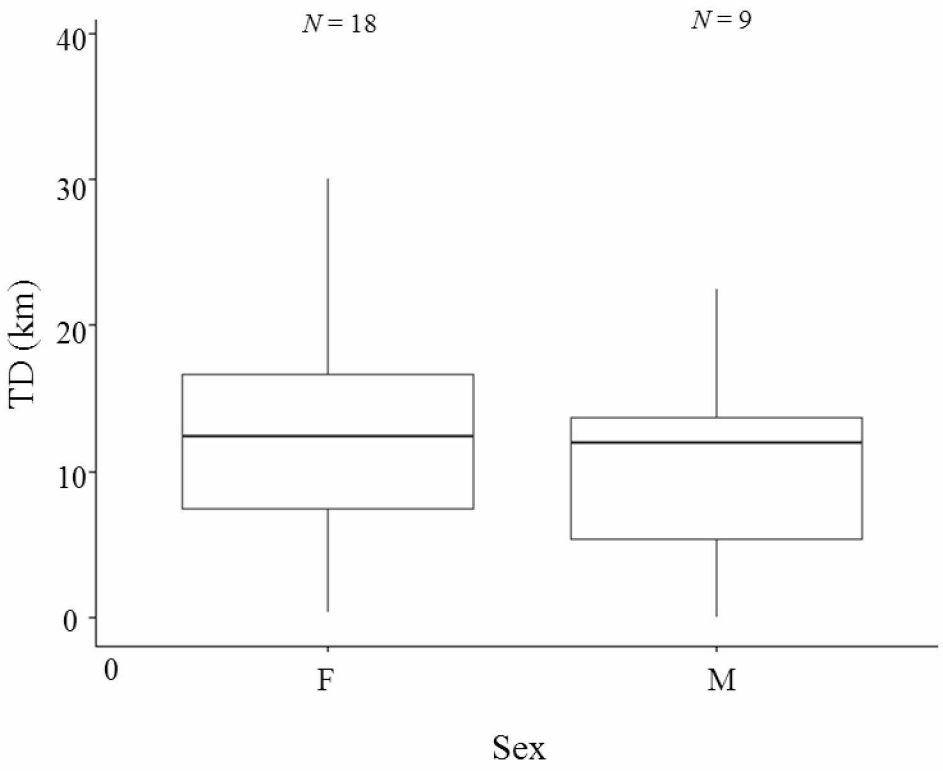

Fig. 2.3. Mean total distance traveled (km) by telemetry-tagged rainbow trout in Willow Creek study area during the summer feeding season by sex. Boxes represent the 25th and 75th percentiles, whiskers the 10th and 90th percentiles, solid lines the median, and dots indicate outliers. Only individuals with five weeks or more of telemetry locations were included in the total movement analysis.

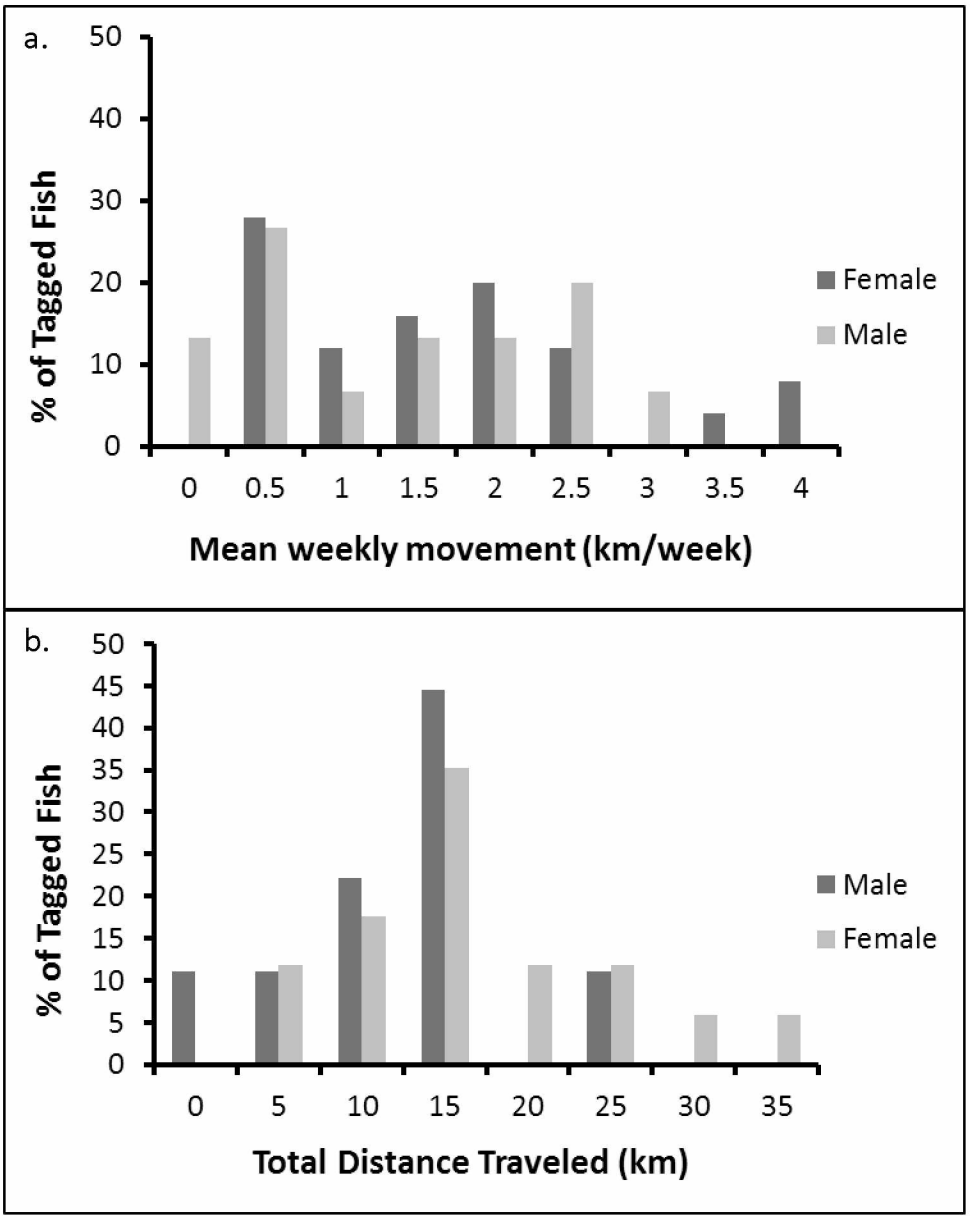

Fig. 2.4. Frequency of mean weekly movement (km/week; a.) and total distance traveled (km; b.) by radio-tagged rainbow trout in Willow Creek, Alaska during the summer feeding season by sex. Only individuals with five weeks or more of telemetry locations were included in the total movement analysis.

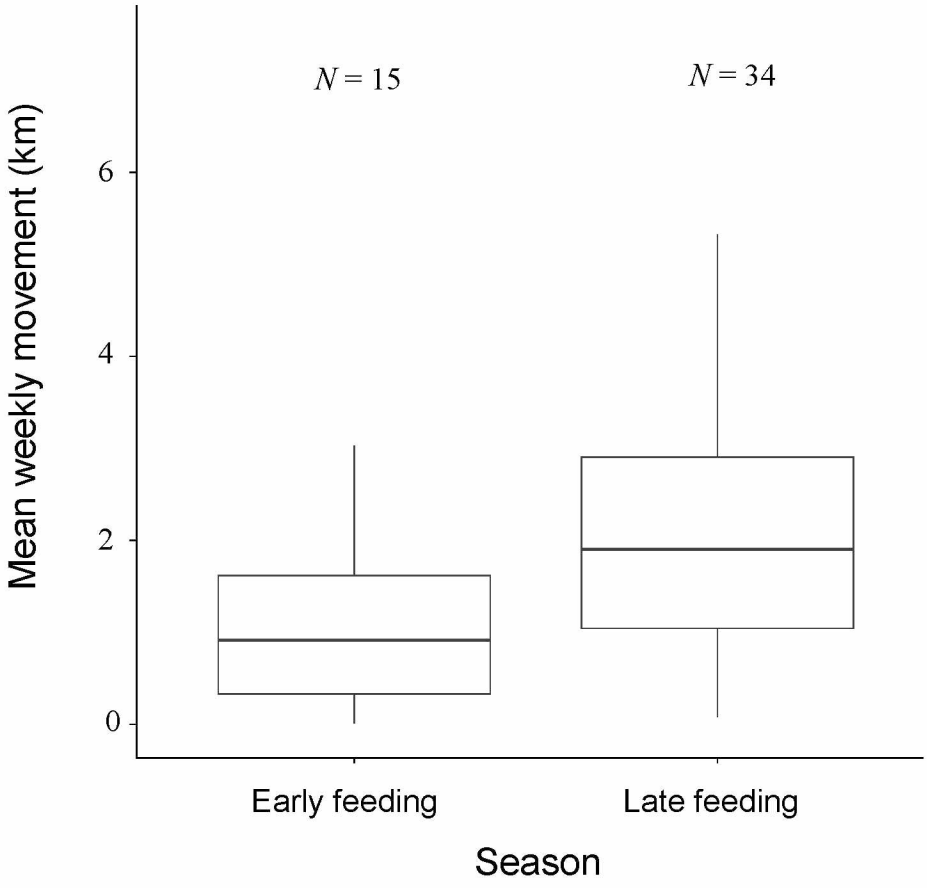

Fig. 2.5. Willow Creek telemetry-tagged rainbow trout mean weekly movements (km) by season. Boxes represent the 25th and 75th percentiles, whiskers the 10th and 90th percentiles, solid lines the median, and dots indicate outliers.

Table 2.1. Summary of rainbow trout habitat characteristics measured or calculated for the Willow and Deception Creeks, Alaska study area. Abbreviations and examples or units are shown. See methods section for descriptions.

Spatial Scale	Data Source	Description	Abbreviation	Example or Units
Channel unit	Field-collected	Channel unit type	CLASS	Pool, riffle, run
		Channel unit sub-type	SUBCLASS	Plunge pool, rapid, etc.
		Maximum depth	MAXD	cm
		Mean depth	DEP	cm
		Wetted channel width	WW	m
		Bankful channel width	BFW	m
		Dominant substrate	SUB	Silt, sand, gravel, etc.
		Percent large woody debris coverage	LWD	%
		Gradient	cuGRAD	%
		Channel unit length	LEN	m
		Channel unit volume	VOL	m^3
		Salmon presence	SALM	Yes or no
		Salmon species richness	SALMR	Species count
Stream reach	Field-collected	Percent of channel units with salmon present	SALMP	% of channel units
		Number of pool channel units	POOLS	Count per reach
	NetMap	Mean annual flow	MAF	m^3/s
		Sinuosity	SINU	Unitless
		Gradient	rchGRAD	%

Table 2.2. Summary of size and habitat use (by habitat classification, Table 2.1) for telemetry-tagged rainbow trout in the Willow Creek study area, Alaska by sex and year. The number of fish tagged, mean, minimum, maximum, and standard deviation of fork length (mm); the number of fish that survived tagging and gave one or more live signals (Live); and 'Pool,' 'Riffle,' and 'Run' denote the proportion of tagged fish captured in each habitat type.

				Fork length				*Channel unit type*		
Sex	Year	N	Live	Mean	Min	Max	SD	Pool	Riffle	Run
M	2013	16	11	451.88	409	515	31.27	0.50	0.19	0.31
	2014	12	7	468.92	415	521	30.91	0.25	0.42	0.33
F	2013	27	10	462.48	401	545	40.71	0.44	0.22	0.33
	2014	27	17	470.81	405	660	54.73	0.33	0.48	0.19

Table 2.3. Summary of model selection statistics for logistic regression models of adult rainbow trout snorkel survey detection probability of adult rainbow trout in Willow Creek, Alaska. Covariates include water clarity (WAT; clear or fair), observer (OBS; 1 or 2), water temperature (TEMP; °C), weather (WEATH; sunny, partly cloudy, overcast), max depth (DEPTH; cm), and large woody debris percent coverage (LWD). Fifty-four snorkel surveys were included in this analysis.

Model	L-L	AICc	ΔAIC	w_i	*K*
DEPTH, WAT	-27.02	60.5	0	0.11	3
DEPTH, WAT, TEMP	-26.31	61.4	0.90	0.07	4
DEPTH	-28.71	61.7	1.14	0.06	2
DEPTH, TEMP, LWD, OBS	-25.23	61.7	1.19	0.06	5
DEPTH, WAT, LWD	-26.52	61.9	1.33	0.06	4
DEPTH, LWD	-27.88	62.2	1.71	0.05	3
DEPTH, LWD, OBS	-26.80	62.4	1.88	0.04	4
DEPTH, WAT, OBS	-28.00	62.4	1.89	0.04	4
DEPTH, OBS	-25.63	62.5	1.95	0.04	3
DEPTH, WAT, TEMP,OBS	-25.70	62.5	1.99	0.04	5
DEPTH, WAT, TEMP,OBS, LWD, WEATH (global model)	-24.41	68.00	7.49	<0.01	8

Table 2.4. Model-averaged parameter estimates and unconditional 90% confidence intervals for top models (AICc $w_i > 0.05$; Table 2.3) of snorkel survey detection probability of adult rainbow trout as a function of covariates in channel units where telemetry-tagged fish were known to be present in the Willow Creek study area, Alaska. See 'Methods' for description of covariates.

Parameter	Estimate	Lower 95% CL	Upper 95% CL
OBS:1, WAT:clear (Intercept)	-3.08	-8.10	1.94
DEPTH	0.02	0.004	0.04
OBS:2	-2.01	-3.68	-0.34
WAT:fair	-1.38	-2.67	-0.10
TEMP	0.32	-0.08	0.72
LWD	0.03	-0.008	0.06

Table 2.5. Summary of model selection statistics for top habitat use models for adult rainbow trout in Willow Creek study area, Alaska. Abbreviations are as follows: L-L =log-likelihood; ΔAIC_c= difference in the corrected Akaike information criterion (AIC_c) value for a particular model compared with the top-ranked model; and K = the number of parameters, including the intercept and residual variance. Parameters are abbreviated as outlined in Table 2.1

Scale	Model	L-L	AICc	ΔAICc	w_i	*K*
Channel unit	DEP, LEN, WW, VOL, SALM	-121.79	255.99	0.00	0.53	6
Channel unit	DEP, LEN, WW, VOL, SALM, SEASON	-121.57	257.69	1.70	0.23	7
Combined	DEP, LEN, WW, VOL, SALM, SEASON, SALMR, MAF, SALMP (global model)	-118.64	258.39	2.40	0.16	10
Combined	DEP, LEN, WW, VOL, SALM, MAF, SALMP	-121.41	259.54	3.55	0.09	8
Channel unit	DEP, LEN, WW, VOL	-132.19	274.68	18.69	<0.01	5
Stream reach	MAF, SALMP	-134.83	275.77	19.78	<0.01	3
Channel unit	SALM, SALMR, SEASON	-133.97	276.14	20.15	<0.01	4
Combined	DEP, LEN, WW, VOL, MAF	-132.10	276.62	20.63	<0.01	6
Stream reach	MAF, SALMP, SEASON	-134.80	277.81	21.81	<0.01	4
Channel unit	DEP, LEN, WW, VOL, CLASS, GRAD, SEASON	-129.55	278.015	22.02	<0.01	9

Table 2.6. Model-averaged parameter estimates and lower and upper 90% confidence limits (CLs) for covariates predicting habitat use of rainbow trout in the Willow Creek study area, Alaska. Estimates are derived from the confidence set of models with w_i>0.05 (Table 2.5).

Scale	Parameter	Estimate	Lower 95% CL	Upper 95% CL
Combined	SEASON:early (Intercept)	-4.08	-5.42	-2.74
Channel unit	SALM	1.66	0.81	2.50
Channel unit	SALMR	-0.73	-1.28	-0.17
Channel unit	DEP	0.05	0.03	0.07
Combined	SEASON:late	-0.11	-0.68	0.46
Channel unit	LEN	0.009	<0.01	0.01
Channel unit	VOL	-0.001	-0.008	0.06
Channel unit	WW	0.03	> -0.01	0.06
Stream reach	MAF	0.02	-0.04	0.08
Stream reach	SALMP	-0.46	-1.72	0.79

Table 2.7. Mean condition factor (*K*) and relative weight (*Wr*) for a subset of rainbow trout captured before and after peak salmon spawning abundance in Willow Creek, southcentral Alaska. Optimal condition value is 1 for *K* and 100 for *Wr*. Means were compared using single factor ANOVA. Peak salmon spawning abundance was observed to be August 15, 2013.

Index	Season	Mean	N	*p*
Wr	Before	81.62	13	<0.01
	After	103.89	13	
K	Before	1.11	13	<0.01
	After	1.39	13	

Appendix

APPENDIX 2.A. Spawning dynamics of rainbow trout in Willow Creek, Alaska

Methods

Because spawning and non-spawning areas were known in the Willow and Little Willow Creek drainages based on snorkel observations and sampling (K. Fraley, *personal observation*; Fig. 1.1), we determined whether trout from Willow Creek observed in 2004 and 2014 spawned or had abstained from spawning (skipped spawning; Rideout and Tomkiewicz 2011). Fish that were located in Deception Creek or Upper Little Willow Creek (Fig. 2.A.1) were determined to have spawned, whereas individuals that remained in Lower Willow Creek were designated as non-spawners; no redds were ever observed in Willow Creek during two seasons of detailed snorkeling and habitat assessment (K. Fraley, *personal observation*).

Results/Discussion

The proportion of Willow Creek 2014 trout that spawned was 60%; 30% did not spawn, and 10% were missing during the spawning season (n=20; Fig. 2.A.2). For the 2004 Willow Creek sample (N=27), 55.6% of fish spawned, non-spawners made up 37%, and 7.4% of trout were found in locations where it was unknown if spawning occurred (Fig. 2.A.1).

During the spawning season in 2014 70% of male fish (N = 10) and 50% of female fish (N = 10) spawned. Both male and female samples exhibited a 30% non-spawning rate because 20% of females were missing during this time period (outside of study area, returned during feeding season). In the trout that did spawn, post-spawning mortality was higher for males (42.9%, N = 7) compared to females (20%, N = 5) in the 2013 sample, while the spawning season was not observed for the 2014 sample. Sex was not determined for the 2004 sample.

It is likely that fewer females spawned because the energy thresholds required to produce eggs are higher than for males to produce sperm. Thus, females would be more likely to skip spawn (Rideout et al. 2005). Male post-spawning mortality may be higher due to longer time guarding the redd and greater effort invested in spawning activity (intrasexual competition and redd defense; Hutchings 1994; De Gaudemar 1998; K. Fraley, *personal observation*) compared to females. Within Willow Creek, an angling closure protects rainbow trout during the spawning period in Deception Creek. However, trout spawning areas in upper Little Willow Creek (Fig. 2.A.1, Fig. 2.A.2) do not have similar protection. It may be prudent for managers to identify and

protect trout spawning habitat in Little Willow Creek and other Susitna River tributaries because trout are particularly vulnerable to and easily stressed by angling during the critical spawning period.

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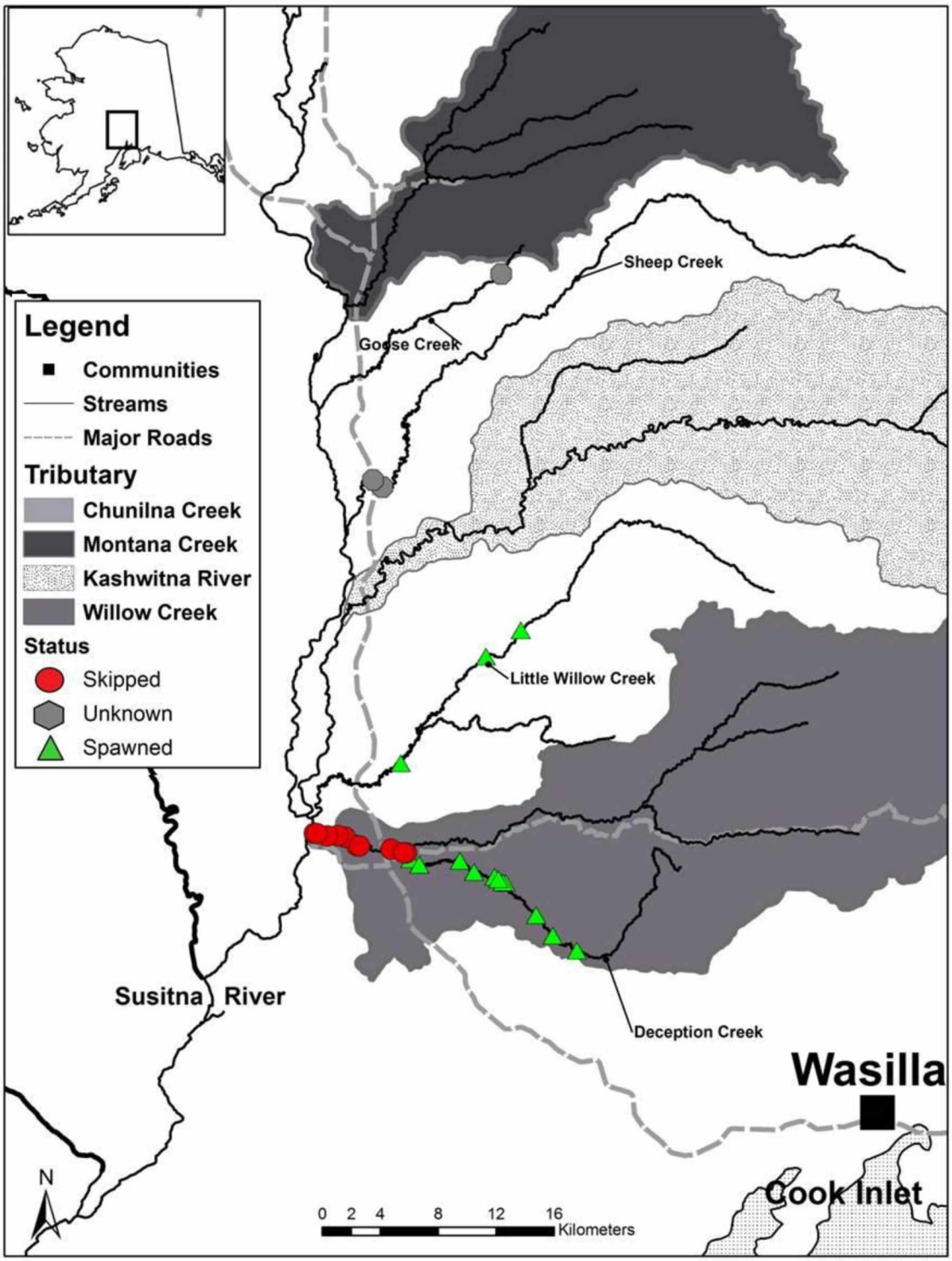

Fig. 2.A.1. Rainbow trout locations during the spawning season for fish tagged in Willow Creek, Alaska in 2003.

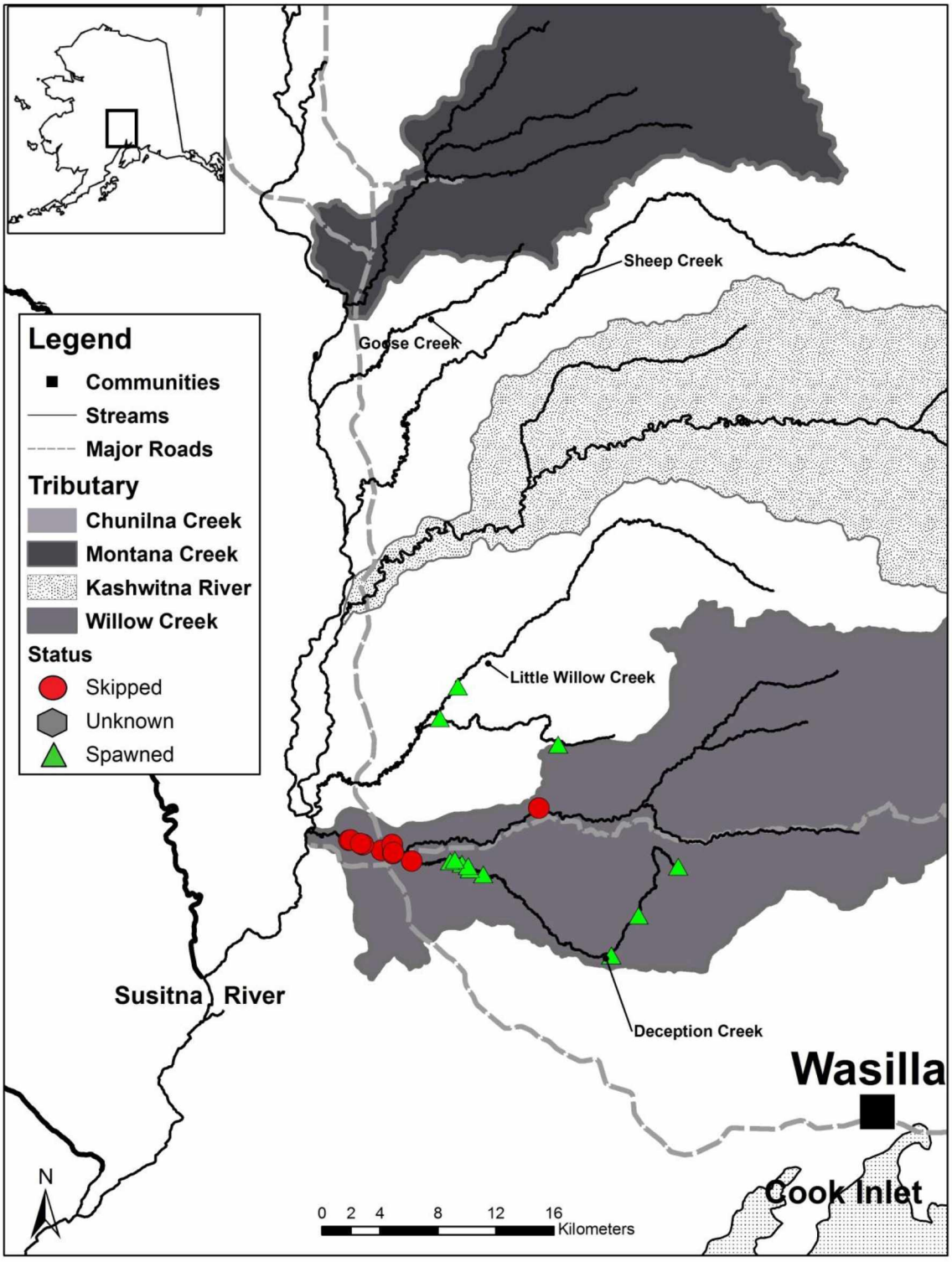

Fig. 2.A.2. Rainbow trout locations during the spawning season for fish tagged in Willow Creek, Alaska in 2014.

Conclusions

We characterized habitat use and movements of potamodromous Rainbow Trout within a complex, glacially influenced river basin at multiple spatial and temporal scales. Findings from chapter one indicated that over the course of a year Susitna River basin trout moved long distances and occasionally utilized multiple tributaries within and among seasons. Inter-tributary movements suggest a basin-wide metapopulation and heterogeneity in trout movements. Habitat use by trout varied across seasons, with individuals selecting stream reaches with characteristics supporting refuge from harsh overwinter conditions, spawning in the spring, and feeding over summer months. In general, individuals exhibited a novel seasonal movement pattern where they overwintered in glacially-influenced mainstem reaches during the long ice-covered season from October through May, moved into upper reaches of clearwater tributaries during the spawning season from mid-May to early June, and remained in tributaries to feed from mid-June through September. Movements varied among seasons, with the longest mean distance traveled being from overwintering to spawning.

In chapter two we found that Rainbow Trout exhibit differential habitat selection over multiple spatial scales. In the case of Willow Creek Rainbow Trout, fish responded to finer-scale (channel unit) characteristics rather than more coarse-scale (stream reach) variables. The presence of salmon, increasing mean depth, and longer reach length were particularly useful positive predictors of habitat use, while trout selected against increased salmon richness (possibly due to avoidance of large aggregations of aggressive pink salmon). There was no evidence at either the weekly or seasonal (early and late feeding) temporal scales of sex-biased movements. However, weekly movements averaged over individuals were significantly longer during the late feeding season when spawning salmon were present. The proportion of females deemed less mobile was high across both early and late feeding seasons, while males were more sedentary pre-salmon arrival and equally split between sedentary and mobile strategies in the late feeding season.

Differences in habitat variable values (particularly the range of values) at different spatial scales were seen within NetMap. NetMap attributes at the Susitna River basin scale (chapter one) showed a range of values and were not significantly correlated with each other when variance inflation factors (VIF) were calculated. However, within the Willow and Deception Creeks study area (chapter two), the values for several of the variables had a narrow range (i.e,.

low contrast) and were highly correlated with each other (VIF > 10), rendering them less useful for explaining reach-scale habitat use of Rainbow Trout. This is likely due to the resolution of the data informing the habitat models and the suitability of the models themselves at varying scales, and highlights the importance of selecting habitat datasets at the appropriate scales for the analysis desired.

The Kashwitna River Rainbow Trout subpopulation may be an important vector of gene flow in the Susitna River basin owing to the prevalence of long-distance and out-of-tributary movements by trout from this drainage. Additionally, the propensity of Kashwitna River trout to undertake movements away from their tributary of capture may indicate low-quality or limited availability of seasonal habitats in this drainage, potentially owing to the substantial glacial influence (turbidity) in this tributary. Higher turbidity may result in reduced sight distance for trout, lowering feeding efficiency and increasing the difficulty in locating conspecifics for mating, which may prompt movements to less-turbid tributaries. High tributary fidelity in Willow, Montana, and Chunilna Creeks suggests there is an abundance of quality habitats available for trout in these drainages across seasons. As a result of possible metapopulation dynamics, it is critical to manage Rainbow Trout at a basin-wide scale and maintain riverscape connectivity in order to account for the migratory nature of these diverse subpopulations. The Alaska Department of Fish and Game Rainbow Trout management approach has evolved over the last several decades, with recent emphasis on conservative harvest limits and catch-and-release angling to promote healthy populations and trophy trout fisheries (Bartlett and Hansen 2000). However, significant harvest of Rainbow Trout still occurs in the Susitna River basin, and the effect of heavy catch-and-release angling, as evidenced by the presence of hooking scars on about one-third of all captured fish, may increase stress on fish, cause exhaustion, and result in higher risk of mortality.

Spawning salmon presence influences habitat use and movements for potamodromous Rainbow Trout. Trout likely rely on high-calorie salmon-derived food subsidies to gain fat and energy reserves in order for survival during the winter months and gonadal development the following spring (Scheuerell et al. 2007; Armstrong and Bond 2013). Thus, the abundance of salmon-derived food items (and also adult salmon) has implications on trout fitness (survival, reproductive success) and river carrying capacity (total food availability, invertebrate secondary production) for Rainbow Trout (Denton et al. 2009; Rinella et al. 2011). Because of the potential

importance of spawning salmon to Rainbow Trout population health, it is important that salmon are not overharvested and are kept at population levels high enough to avoid detrimental effects on non-anadromous salmonids (Eastman 1996, Scheuerell et al. 2007, Denton et al. 2009). However, a significant proportion of salmon populations are currently declining across Alaska and the Pacific Northwest region (Hilborn 2013). In order to foster ecologically and economically important trout populations while still allowing for a reasonable commercial catch of salmon, all resource users must make equal compromises to ensure the preservation of healthy salmon populations (Eastman 1996, Denton et al. 2009). This may include decreased salmon and trout quotas and bag limits for commercial and sport fisherman and the utilization of substitute food items for subsistence users during times of low salmon abundance. In addition, protection of salmon spawning and rearing habitats in freshwater in Alaska will be important in light of future climate change and human development such as urbanization and installation of hydropower dams, which may have cascading effects on salmon (and also trout) freshwater habitats (Prowse et al. 2006; Schick 2006; AEA 2013; MSBSHP 2013). Moving into the future it will also be important to regularly monitor salmon abundance and habitat use at multiple spatial scales to identify and address potential threats (Fausch et al. 2002).

Another factor that may influence Rainbow Trout in the Susitna River basin is increased anthropogenic impacts in the region. This includes accelerated global change in the sub-Arctic, the proposed Susitna-Watana Hydropower Project, human population expansion, road building, clearing of riparian vegetation, and fish passage issues (Prowse et al. 2006; AEA 2013; MSBSHP 2013). Road building and riparian alteration could cause siltation and higher water temperatures in tributaries containing Rainbow Trout. This could be particularly harmful during spawning if siltation smothered eggs in redds or increased temperatures caused deleterious changes in egg incubation and juvenile trout growth. Global change trends may also cause warmer water temperatures, altered seasonal timing, risk of wildfires, and increased flooding or drying events. It is unknown what the effect of this might be on Rainbow Trout, but non-natural disturbances often are threats to stable native fish populations (Dunham et al. 2003). The Susitna-Watana hydropower dam, currently in the planning and environmental assessment stage, would likely cause far-reaching effects in the Susitna River from dam operations that may include altered flow and thermal regimes and changes in turbidity, with effects on aquatic habitat in the mainstem Susitna River downstream of the site (Devil's Canyon in the upper basin; AEA

2013; WDAFS 2015). The potential effects of this dam on salmon and non-anadromous fish populations (including Rainbow Trout) in the Susitna Basin are currently unknown but are the focus of significant research efforts. Baseline research from the current study that identifies and quantifies seasonal habitats of fish and wildlife potentially affected by development is important for before-after comparisons and monitoring. Overwintering habitat is of particular concern for Rainbow Trout downstream of the dam site because a high proportion of tagged fish from all tributaries used the mainstem Susitna River during this season. Our research showed that overwintering trout select areas with increased sinuosity and mean annual flow (stream size), habitat characteristics that likely would be affected by the alteration of flows and loss of seasonal flood events that shape channel geometry (Ligon et al. 1995; Gordon and Meentemeyer 2006). If winter base flows and water temperatures increase following dam construction, overwintering Rainbow Trout may be affected through increased energy expenditure from higher metabolic rates (WDAFS 2015).

We would recommend that research examining watershed or basin-scale aquatic habitat utilize NetMap, as it appears to be suitable and useful at a broad spatial scale (10^3 m and greater). Researchers are cautioned that NetMap may be less useful for fine scale studies because of high correlation between habitat attributes and a narrow range of attribute values. Intensive field measurements are most accurate for fine spatial scales, but are time-consuming and impractical over large stream systems or in remote areas. An alternate approach would be to use remotely-sensed high resolution orthoimagery and classify habitat types and calculate variables such as sinuosity, LWD percent cover, and depth (Smikrud et al. 2008; Woll et al. 2011). This was explored for Willow and Deception Creeks, but ultimately field measurements were used instead. Measurements in the field were feasible for this research because of ease of access to the stream (on the road system) and budgeted time and man-power for this endeavor. For aquatic habitat research that is time-limited or has a study area that is less accessible, orthoimagery classification and analysis may be a better approach (Smikrud et al. 2008; Woll et al. 2011).

Future Rainbow Trout research in the Susitna River basin could examine the influences of seasonal and daily flows and water temperatures recorded from USGS streamgage or using a set of field-installed temperature loggers on trout movements and habitat use across tributaries. These data were available for some of the Susitna River basin study area, but the analysis was outside the scope of our effort and objectives. Additionally, the suggested metapopulation dynamics and female-

biased sex ratio could be further studied by conducting a genetics survey of juvenile Rainbow Trout from various Susitna, Talkeetna, and Chulitna River tributaries. This approach could quantify genetic difference and mixing as well as at-birth sex ratios throughout the basin. The results of these possible avenues of research would likely be very valuable for understanding and management of Susitna Rainbow Trout.

In summary, this research contributes to a better understanding of potamodromous Rainbow Trout movements and habitat use, and findings may be applicable to other river systems in Alaska and the Pacific Northwest. Native Rainbow Trout are an important ecological and recreational resource in freshwater systems of Alaska that need to be carefully conserved and managed as declining salmon stocks, increased development, hydroelectric projects, and global change threaten their populations.

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Appendices

Appendix A. 2013 IACUC approval

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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

June 12, 2013

To:	Jeffrey Falke, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[450318-2] Characterization of resident rainbow trout seasonal habitats in Willow Creek, Alaska

The IACUC reviewed and approved the Amendment/Modification to protocol documents referenced above by Designated Member Review.

Received:	June 3, 2013
Approval Date:	June 12, 2013
Initial Approval Date:	June 12, 2013
Expiration Date:	June 12, 2014

This action is included on the June 20, 2013 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

Appendix B. 2014 IACUC approval

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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

May 29, 2014

To:	Jeffrey Falke, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[450318-4] Characterization of resident rainbow trout seasonal habitats in Willow Creek, Alaska

The IACUC has reviewed the Progress Report by Designated Member Review and the Protocol has been approved for an additional year.

Received:	May 23, 2014
Initial Approval Date:	June 12, 2013
Effective Date:	May 29, 2014
Expiration Date:	June 12, 2015

This action is included on the June 12, 2014 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures detailed in the form 005 "Reporting Concerns".*